

THE EFFECTS OF MAMMALIAN HERBIVORES ON  
SUCCESSIONAL GRASSLANDS IN CENTRAL ILLINOIS

BY

CARRIE ELIZABETH DEJACO

B.A., University of Louisville, 1996

M.S., University of Louisville, 2000

DISSERTATION

Submitted in partial fulfillment of the requirements  
for the degree of Doctor of Philosophy in Biology  
in the Graduate College of the  
University of Illinois at Urbana-Champaign, 2006

Urbana, Illinois

## ABSTRACT

No previous study has separated the effects of several types of herbivorous mammals on mid-western grassland communities at different stages of development, in spite of a substantial literature indicating the potential of mammals to impact the composition of these plant communities. Mice and voles consume large seeds, and rabbits disperse small seeds endozoochorously. Voles, rabbits, and deer prefer certain plant species, particularly leguminous forbs, over graminoids. Deer, rabbits, and voles often damage woody plants and seedlings. I therefore expected fewer small-seeded plants in areas without access by rodents and rabbits, greater abundances of palatable plants in areas without access to each herbivore, and more woody seedlings in areas without access to each herbivore. I expected effects of granivory and endozoochory to be stronger in early succession than in mid- or late succession because plant recruitment by seeds is more important in early succession.

I used exclosures that allowed access to different combinations of animals to assess the impact of mice, voles, rabbits, and deer in old fields of 3 successional stages. In addition, I conducted feeding trials to determine palatabilities of plants and seeds to the most abundant small mammal species (*Peromyscus leucopus*, *Microtus ochrogaster*, *M. pennsylvanicus*, and *Sylvilagus floridanus*) and related these data to those from the exclosure experiments. To determine the kinds and numbers of plants commonly dispersed by rabbits, I also collected and germinated plants from rabbit fecal pellets.

Neither rabbit endozoochory nor rodent granivory affected plant communities in any successional stage. Rodents did not prefer larger seeds. Herbivory by rabbits and rodents influenced the plant communities more than did consumption or dispersal of seeds. Both

groups of animals reduced abundance of palatable forbs and increased that of unpalatable forbs. Grasses palatable to voles increased in exclosures during mid- and late succession. Rodent exclusion also significantly increased abundance of the legume *Medicago sativa*, which had highly palatable shoots and seeds. *Cirsium arvense*, a palatable forb, increased substantially with the removal of deer and the grass *Festuca arundinacea* declined. Woody seedlings rarely occurred in the grasslands and none of the mammals affected their abundance.

*This is dedicated to my advisor,  
Who challenged me and chided me,  
Inspired me and guided me,  
But never, ever, ever  
Would he let me "Be".*

## ACKNOWLEDGEMENTS

I would like to acknowledge all of those who helped inspire and motivate me, those who assisted me and supported me, in no particular order: my mom and grandma; my advisor, George Batzli, for being the best role model a person could imagine and for sharing with me his endless knowledge in the field, helping me find meaning amidst the pages and pages of data, and patiently guiding my writing; Ed Heske, my "second in command" advisor, for his guidance, stimulating conversation, and sustenance; my other committee members, Jeff Brawn and Ben Tracy for their support through it all; my 19 undergraduate field assistants (especially Melinda Peddycoart, Agnieska Sukiennik, and Amy Trowbridge) without whom I would have been hopelessly overwhelmed with the work in the field; everyone else who assisted me with construction (and who hopefully will assist with deconstruction!) in the field and/or provided wonderful and stimulating scientific conversation (including, but not limited to Suzanne Beyeler, Dave Chalcraft, Jenny Duggan, Sue Gallo, Beth Gault (now Gilson), Dan Harvey, Scott Kelly, Molly McNicoll, Eli Saetnan, Jenn Smith, Jeff Steinmetz, Heather Vance). Each one of you contributed your confidence in me, which helped me believe that I could do it. Thank you!

## TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION .....	1
Literature Cited .....	9
CHAPTER 2: THE INFLUENCE OF RABBITS ( <i>Sylvilagus floridanus</i> ) ON THE COMPOSITION OF SUCCESSIONAL GRASSLANDS .....	16
Introduction.....	16
Methods.....	18
Results.....	25
Discussion.....	32
Literature Cited .....	36
CHAPTER 3: EFFECTS OF HERBIVORY AND GRANIVORY BY MICE ( <i>PEROMYSCUS spp.</i> ) AND VOLES ( <i>MICROTUS spp.</i> ) IN SUCCESSIONAL GRASSLANDS.....	46
Introduction.....	46
Methods.....	48
Results.....	56
Discussion.....	63
Literature Cited .....	70
CHAPTER 4: EFFECTS OF WHITE-TAILED DEER ( <i>Odocoileus virginianus</i> ) ON SUCCESSIONAL GRASSLANDS .....	82
Introduction.....	82
Methods.....	83
Results.....	87
Discussion.....	91
Literature Cited .....	94
CHAPTER 5: CONCLUSIONS .....	101
Literature Cited .....	109
APPENDIX A. Statistical tables for repeated measures ANOVA testing hypotheses regarding rabbit access. ....	116
APPENDIX B. Statistical values of Mann-Whitney analyses of individual plant species' response to rabbit access.....	131
APPENDIX C. Statistical tables for repeated measures ANOVA testing hypotheses regarding rodent access .....	134

APPENDIX D. Statistical values of Kruskal-Wallis analyses of individual plant species' responses to rodent access .....	145
APPENDIX E. Statistical tables for repeated measures ANOVA testing hypotheses regarding deer access.....	148
APPENDIX F. Statistical values of Mann-Whitney analyses of individual plant species' response to deer access .....	152
APPENDIX G. Means and standard errors for all plant species for fall seasons, 2001 through 2004.....	155
CURRICULUM VITAE .....	166

## CHAPTER 1

### INTRODUCTION

*Background.*— Early successional change in vegetation after release of old fields from agriculture is well known for the eastern half of the United States (Bazzaz 1996, pp. 38-43) and clear developmental patterns also occur in small mammal communities as old field succession progresses (Foster and Gaines 1991; Bowers 1993; Churchfield, et al. 1997). Annual grasses and short-lived herbs dominate during the first few years, but are quickly replaced by perennial herbs and rhizomatous graminoids. Woody shrubs and trees slowly invade and within two to three decades, a woodland has begun to develop. These changes in vegetation are usually thought to be caused by differences in dispersal, growth rates, and resource use among plant species (Connell and Slayter 1977; Tilman 1985). Frequently in the midwestern U.S.A., management practices (mowing or fire) prevent invasion by shrubs and trees, making it likely that old field grasslands will remain an important ecosystem across the Midwest.

In Illinois, over 99.9% of the original 8.5 million hectares of tallgrass prairie are gone (IDENR 1994), but grasslands still account for 19.2% of current land cover in Illinois (CTAP 2001). The majority of these grasslands are dominated by non-native grasses and are in the form of old fields, pastures, buffer strips along agricultural fields, or maintained roadsides. Good management of grassland ecosystems requires a thorough understanding of the interactions between plants and animals.

A variety of abiotic and biotic factors influence the development of grasslands. Climate, soil type, amount and frequency of precipitation, nutrient availability, and



disturbance dictate which plant species have the potential to live in an area (Howe 1995, Ritchie and Tilman 1995, Treiber 1999, Lane et al. 2000). Animal activities such as wallowing, burrowing, and waste deposition increase habitat heterogeneity, enabling a greater number of plant species to coexist within a field (Huntly and Reichman 1994, Knapp et al. 1999). Herbivory by mammals can alter plant community composition depending on the intensity, duration, and selectivity of grazing. As a result, increased abundance of unpalatable species, increased primary production via overcompensatory growth by plants, or even increased abundance of highly palatable species can occur (McNaughton 1985, Swihart 1991, Frank and McNaughton 1993, English and Bowers 1994, Ritchie and Tilman 1995, Augustine and McNaughton 1998, Olff and Ritchie 1998, Howe and Brown 1999).

Knapp et al. (1999) reported that the dominant herbivores in tallgrass prairies (bison), through grazing and other activities, are keystone organisms in tallgrass prairies. Bison are no longer a free-ranging component of grassland communities in Illinois, but other native mammalian herbivores remain. White-tailed deer (*Odocoileus virginianus*) are the largest of remaining herbivores in Illinois grasslands (Hoffmeister 1989). Although no precise estimates of their abundance prior to European settlement exist, their populations had declined by the early 1900s to the point that conservation became an issue (Russell et al. 2001). Woody landscapes were fragmented into habitats more favored by deer and restrictions were placed on harvests by hunters (Russell et al. 2001). As a result of these measures and the extirpation of most of their natural predators (Diamond 1992), deer populations have reached record highs across most of the eastern half of North America (Nixon et al. 2001).

The eastern cottontail rabbit (*Sylvilagus floridanus*) also commonly occurs in Illinois grasslands (Mankin and Warner 1999), although estimates of rabbit populations from hunter harvests have indicated declines over the past 40-50 years. That trend may reflect the loss of optimal habitat and changes in the landscape (Sole 1995, Roseberry 1998). While both the rabbit and deer use diverse, patchy landscapes that include agricultural fields and grasslands for foraging and wooded areas for shelter, the rabbit prefers to find shelter in brushier habitat such as fence rows or hedge rows. In addition, many smaller carnivores that commonly prey on rabbits are increasing across the landscape (Goodrich and Buskirk 1995, Ray 2000).

Populations of prairie and meadow voles (*Microtus ochrogaster* and *M. pennsylvanicus*), the smallest mammalian herbivores in midwestern grasslands, do not seem to have increased or decreased in abundance recently, other than the typical multi-annual fluctuations (Getz et al. 2001). Mice (*Peromyscus spp.*, *Reithrodontomys megalotis* and *Zapus hudsonius*), although generally not herbivorous, are major seed predators (Gossard 1923, Quimby 1951, Whitaker and Mumford 1972; Mittelbach and Gross 1984) and, as common inhabitants, they may also directly influence plant communities in old fields. *Peromyscus spp.* are particularly common in grassland areas near woodlands, while *R. megalotis* and *Z. hudsonius* are less abundant in Illinois grasslands and occur sporadically (Hoffmeister 1989, Falout and Nelson 1997).

Studies on the influences of white-tailed deer in woodlands have found that browsing on tree seedlings and saplings can alter the species composition within the plant community, leaving the less palatable species to dominate (Anderson and Katz 1993, Augustine and Jordan 1998, Gill and Beardall 2001, Rooney and Waller 2003). Deer also forage preferentially on herbaceous understory vegetation in forests and can even eliminate

preferred species (Waller and Alverson 1997, Russell et al. 2001, Rooney and Waller 2003). Although deer frequently forage in early successional areas, relatively few studies have investigated the role of deer in non-woodland habitats (Russell et al. 2001). Some studies in successional grasslands have shown negative effects of deer browsing on growth rates of woody seedlings and saplings, which can slow the rate of succession (Inouye et al. 1994, Knapp et al. 2002), but I found only 2 studies by Anderson et al. (2001, 2005) that investigated the effects of deer on non-woody plants in grasslands. They found that deer exclosures in tallgrass prairie remnants in northern Illinois had decreased abundance of unpalatable forbs and grasses and increased diversity of forbs, standing biomass and reproductive capacities of preferred species.

Rabbits can strongly influence vegetation through a variety of mechanisms. Preferential folivory on certain plants, such as grasses, small annual plants, and legumes, may substantially reduce abundances of the preferred species, leaving the communities dominated by a few unpreferred species (Watt 1962, Sumption and Flowerdew 1985, Crawley 1990). Cullen et al. (1998) reported increased plant cover, richness, and diversity after just one year of rabbit exclusions from reclaimed quarry lands, while Edwards and Crawley (1999) found that excluding rabbits resulted in significantly lower flower-head production in 7 of 9 common species. Rabbits frequently clip tree seedlings and often consume bark during winter months, which can lead to decreased abundance of woody plants (Dusi 1952, Sumption and Flowerdew 1985, Holl and Quiros 1999) and seed dispersal by rabbits in feces (endozoochory) can contribute substantially to both the numbers and species pool of seed banks (Malo and Suarez 1996). Most studies on rabbits' influence on plant communities have been conducted in European grasslands, where rabbit densities seem

consistently higher (2 to >200/hectare; Sumption and Flowerdew 1985, Pakeman et al. 1998) than in the midwestern U.S.A. (<1 to 10/hectare; Mankin and Warner 1999). Schupp et al. (1997) studied seed dispersal by hares and rabbits in the rangelands of the western U.S.A. and concluded that they do not effectively disperse seeds in that habitat. Zedler and Black (1992), however, reported that seed dispersal by rabbits could be crucial to colonization, re-establishment, and gene flow among plants in a semi-arid vernal pool landscape in California.

The feeding habits of voles (*M. ochrogaster* and *M. pennsylvanicus*) in mid-western U.S.A. are well known (Thompson 1965, Zimmerman 1965, Cole and Batzli 1979, Lindroth and Batzli 1984, Marquis and Batzli 1989, Haken and Batzli 1996). In central Illinois, both *M. ochrogaster* and *M. pennsylvanicus* seem to prefer certain dicot species, such as legumes and dandelion, although their diets often consist of greater proportions of the more abundant monocots (Thompson 1965, Zimmerman 1965, Cole and Batzli 1979, Lindroth and Batzli 1984, Haken and Batzli 1996). *Microtus pennsylvanicus* consumes a greater proportion of monocots than *M. ochrogaster*, which has a more varied diet (Zimmerman 1965, Haken and Batzli 1996). *Poa pratensis* was cited as one of the most common food items of both species in multiple studies (Zimmerman 1965, Cole and Batzli 1979, Haken and Batzli 1996), although its nutritional content is not sufficient to maintain voles in the lab (Cole and Batzli 1979). Seeds are an important part of voles' diet, especially in autumn and winter, and *M. ochrogaster* seems to consume more seeds than *M. pennsylvanicus* (Zimmerman 1965, Cole and Batzli 1979, Lindroth and Batzli 1984), but few studies have quantified palatability of seeds to voles. Several studies reported negative effects of voles on tree seedlings in grasslands, which may slow the process of succession (Ostfeld and Canham 1993, Ostfeld et

al. 1997, Manson 2000), but only Howe and Brown (1999, 2000) have reported on the effects of voles on non-woody plants in midwestern grasslands. They found that highly selective consumption of seeds and seedlings by voles in the early stages of tallgrass prairie communities lowered forb biomass and community diversity.

Preference by rodents for particular seeds has been reported by many studies, with large seeds being preferred over small ones, which often leads to increased abundances of smaller-seeded plants (Mittelbach and Gross 1984, Brown and Heske 1990, Samson et al. 1992, Heske et al. 1993, Kerley et al. 1997, Edwards and Crawley 1999; Howe and Brown 2000). Batzli (1977) found that the majority of the *Peromyscus leucopus* diet in the forest was made up of seeds in spring and fall (59-72%) and, even in summer and winter, seeds represented a substantial portion of their diet (26-48%). Katak (1983) reported that *Peromyscus* preferred seeds of weedy grasses (*Setaria* and *Agropyron*) to those of native grasses (*Andropogon* and *Sorghastrum*). Several studies have identified influences of rodent granivory on plant communities in deserts (Brown and Heske 1990; Samson et al. 1992; Heske et al. 1993), and others have documented the presence of granivorous mice in midwestern grasslands (Whitaker and Mumford 1972; Finck et al. 1986; Foster and Gaines 1991; Brillhart and Kaufman 1994), but few have investigated the effects of rodent granivory in midwestern grasslands. One study suggested that, since seed removal rates were higher in undisturbed areas than newly plowed fields, the effects of seed predation on a community may increase as plant succession proceeds (Mittelbach and Gross 1984).

*Objectives and design of study.*— To identify the mechanisms by which herbivorous and granivorous mammals influence non-native grasslands and improve our understanding of development and maintenance of these communities, I conducted exclosure experiments and

feeding trials in 3 old fields representing the development of grassland dominated by non-native species. To help identify changes in mechanisms as succession occurs, I selected 3 old fields of different successional ages: the early successional grassland was released from row crops in fall 2001, the mid-successional was released in 1998, and the late successional was released in 1989 (woody invasion had been prevented until 2001 by regular mowing during the dormant season).

I designed exclosure experiments to separate the effects of different size classes of mammals with a combination of 6 treatment levels allowing access to: 1) all animals— deer, rabbits, voles, and mice (the fenced control); 2) all animals (unfenced control to examine effect of fencing; 3) mice and deer only (no rabbits or voles); 4) mice, voles, and deer (no rabbits); 5) deer only (no small mammals); 6) no deer (accessible to all small mammals). I had three replicates of each treatment level in each of the three fields (Fig. 1.1) and collected data on occurrence and relative cover of plant species by visually examining three permanent 0.5-m by 3-m plots inside each of the 54 treatment plots every spring (May), summer (July), and fall (September) from September 2001 through May 2005. I then compared vegetation for various combinations of treatments to infer the separate effects of deer, rabbits, voles, and mice.

Feeding habits of focal species are relatively well known, but they differ with site and season. Therefore, I conducted feeding trials with the most abundant small mammal species (*Peromyscus leucopus*, *Microtus ochrogaster*, *M. pennsylvanicus*, and *Sylvilagus floridanus*) to determine which of the local plants and parts of plants are preferred by each. I established enclosures maintained in the field so that the animals foraged in natural grassland, exposed to the natural day length and elements. I then related the data on food palatabilities to the data

collected from the exclosure experiments, thereby combining direct knowledge of plant palatabilities with the patterns of vegetational change that occurred in the plant communities over time.

In addition, to determine the kinds and numbers of local plants commonly dispersed by rabbits, I collected deposits of fecal pellets from feeding trial enclosures (representing earlier meals), spread them on trays of soil in the greenhouse, and identified all plants that germinated.

*Significance of study.*— My dissertation research contributes to an overall synthesis of the role of plant-animal interactions in determining the composition of ecological communities by examining the ways in which several species of mammals influence the development and maintenance of old-field grasslands. No previous study has separated the effects of several types of small mammals on grassland communities at different stages of development, nor has any study examined the assemblage of non-native grassland communities in detail.

Results from this research provide a major contribution toward understanding the mechanisms behind the assembly of plant communities in non-native grasslands.

*Organization of dissertation.*— The chapters of this dissertation follow journal format so they may be published as separate papers. The first chapter discusses the effects of herbivory and seed dispersal by rabbits in the three successional stages; the second chapter covers herbivory and granivory by mice and voles, their feeding habits and the changes in vegetation in the three grasslands associated with their activities; and the third chapter addresses the differences in vegetation between areas with and without access by deer. Finally, a concluding chapter summarizes my findings and compares my results to those that others have found using exclosure experiments in other grasslands.

### Literature Cited

- ANDERSON, R. C. and A. KATZ. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. *Biological Conservation* 63: 203-208.
- ANDERSON, R. C., E. A. CORBETT, M. R. ANDERSON, G. A. CORBETT, and T. M. KELLEY. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *Journal of the Torrey Botanical Society* 128: 381-392.
- ANDERSON, R. C., D. NELSON, M. R. ANDERSON, and M. A. RICKEY. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on tallgrass prairie forbs: Diversity and species abundances. *Natural Areas Journal* 25: 19-25.
- AUGUSTINE, D. J. and S. J. McNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. of Wildlife Management* 62: 1165-83.
- AUGUSTINE, D. J. and P. A. JORDAN. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *J. of Wildlife Management* 62: 1076-1085.
- BATZLI, G. O. 1977. Population dynamics of the white-footed mouse in floodplain and upland forests. *American Midland Naturalist* 97: 18-32.
- BAZZAZ, F. A.. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press.
- BOWERS, M. A.. 1993. Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. *Oikos* 67: 129-141.
- BRILLHART, D. E. and D. W. KAUFMAN. 1994. Temporal variation in coyote prey in tallgrass prairie of eastern Kansas. *Prairie Naturalist* 26: 93-105.
- BROWN, J. H. and E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- CHURCHFIELD, S., J. HOLLIER, and V. K. BROWN. 1997. Community structure and habitat use of small mammals in grasslands of different successional age. *J. of Zoology* 242: 519-530.
- COLE, F. R. and G. O. BATZLI. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. *J. of Animal Ecology* 48: 455-470.



- CONNELL, J.H. and R.O. SLAYTER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- CRAWLEY, M. J.. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *J. of Applied Ecology* 27: 803-820.
- CRITICAL TRENDS ASSESSMENT PROGRAM (CTAP). 2001. Critical trends in Illinois Ecosystems. Illinois Department of Natural Resources. Accessed at <http://dnr.state.il.us/orep/ctap2/TOC.pdf>
- CULLEN, W.R., C.P. WHEATER, and P.J. DUNLEAVY. 1998. Establishment of species-rich vegetation on reclaimed limestone quarry faces in Derbyshire, UK. *Biological Conservation* 84: 25- 33.
- DIAMOND, J. 1992. Must we shoot deer to save nature? *Natural History* 101: 2-8.
- DUSI, J.L.. 1952. The food habits of several populations of cottontail rabbits in Ohio. *J. of Wildlife Management* 16: 180-186.
- EDWARDS, G. R. and M. J. CRAWLEY. 1999. Herbivores, seed banks, and seedling recruitment in a mesic grassland. *J. of Ecology* 87: 423-435.
- ENGLISH, E. I. and M. A. BOWERS. 1994. Vegetation gradients and proximity to woodchuck (*Marmota monax*) burrows in an old-field. *J. of Mammalogy* 75: 775-80.
- FALOUT, K. A. and T. A. NELSON. 1997. Small mammal community structure in restored tallgrass prairie. in *Proceedings Fifteenth North American Prairie Conference*, C. Warwick, ed.
- FINCK, E. J., D. W. KAUFMAN, G. A. KAUFMAN, S. K. GURTZ, B. K. CLARK, L. J. McLELLAN, and B. S. CLARK. 1986. Mammals of the Konza Prairie Research Natural Area, Kansas. *Prairie Naturalist* 18: 153-166.
- FOSTER, J. and M. S. GAINES. 1991. Effects of a successional habitat mosaic on a small mammal community. *Ecology* 72: 1358-73.
- FRANK, D. A. and S. J. McNAUGHTON. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* 96: 157-61.
- GETZ, L. L., J. E. HOFMANN, B. McGUIRE, and T. W. DOLAN III. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. *J. of Mammalogy* 82: 22-34.

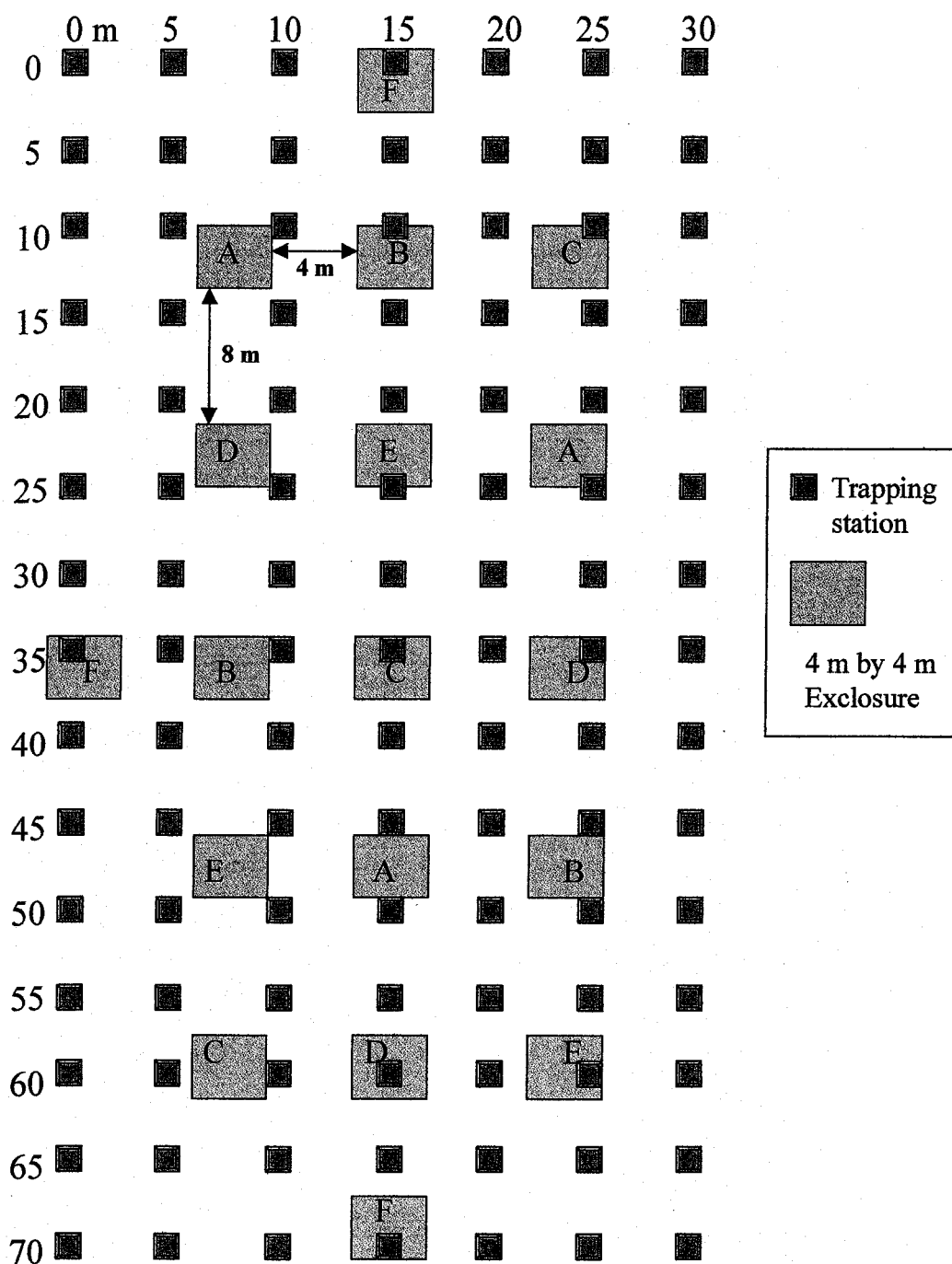
- GILL, R. M. and V. BEARDALL. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:209-218.
- GOODRICH, J. M. and S. W. BUSKIRK. 1995. Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology* 9: 1357-64.
- GOSSARD, H. A.. 1923. Ohio records of the jumping mouse. *Zapus hudsonius*, Zimmerman. Annual Report of the Ohio Academy of Science 23: 284-286.
- HAKEN, A. E. and G. O. BATZLI. 1996. Effects of availability of food and interspecific competition on diets of prairie voles (*Microtus ochrogaster*). *J. of Mammalogy* 77: 315-324.
- HESKE, E. J., J. H. BROWN, and Q. GUO. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95: 520-524.
- HOFFMEISTER, D. F.. 1989. Mammals of Illinois. University of Illinois Press.
- HOLL, K. D. and E. QUIROS-NIETZEN. 1999. The effect of rabbit herbivory on reforestation of abandoned pasture in southern Costa Rica. *Biological Conservation* 87: 391-395.
- HOWE, H. F. 1995. Succession and fire season in experimental prairie plantings. *Ecology* 76: 1917-1925
- HOWE, H. F. and J. S. BROWN. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776-1781.
- HOWE, H. F. and J. S. BROWN. 2000. Early effects of rodent granivory on experimental forb communities. *Ecological Applications* 10: 917-924.
- HUNTLY, N. and O. J REICHMAN. 1994. Effects of subterranean mammalian herbivores on vegetation. *J. Mamm.* 75: 852-9.
- ILLINOIS DEPARTMENT OF ENERGY AND NATURAL RESOURCES (IDENR). 1994. The Changing Illinois Environment: Critical Trends. Summary Report and Volumes 1-7 Technical Report. Illinois Department of Energy and Natural Resources, Springfield, IL, ILENR/RE\_EA\_94/05.
- INOUE, R. S., T. D. ALLISON, and N. C. JOHNSON. 1994. Old field succession on a Minnesota sand plain: Effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club* 121:266-276.
- KANTAK, G.E.. 1983. Behavioral, seed preference and habitat selection experiments with two sympatric *Peromyscus* species. *American Midland Naturalist* 109: 246-52.

- KERLEY, G.I.H., W.G. WHITFORD, and F.R. KAY. 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia* 111: 422-28.
- KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARNETT, L. C. JOHNSON, and E. G. TOWNE. 1999. The keystone role of bison in North American Tallgrass Prairie: bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem process. *BioScience* 49: 39-50.
- KNAPP, A. K., J. M. BRIGGS, J. BOKDAM, and D. J. VAN DER HOEK. 2002. White-tailed deer browsing on six shrub species of tallgrass prairie. *Great Plains Research* 12: 141-156.
- LANE, D. R., D. P. COFFIN, and W. K. LAUENROTH. 2000. Changes in grassland canopy structure across a precipitation gradient. *J. of Vegetation Science* 11: 359-68.
- LINDROTH, R. L. and G. O. BATZLI. 1984. Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. *J. of Mammalogy* 65: 600-606.
- MALO, J. E. and F. SUAREZ. 1996. New insights into pasture diversity: the consequences of seed dispersal in herbivore dung. *Biodiversity Letters* 3: 54-57.
- MANKIN, P. C. and R. E. WARNER. 1999. Responses of eastern cottontails to intensive row-crop farming. *J. of Mammalogy* 80: 940-949.
- MANSON, R. H. 2000. Spatial auto-correlation and the interpretation of patterns of tree seed and seedling predation. *Oikos* 91: 162-74.
- MARQUIS, R. J. and G. O. BATZLI. 1989. Influence of chemical factors on palatability of forage to voles. *J. of Mammalogy* 70: 503-11.
- McNAUGHTON, S. J. 1985. Ecology of a grazing ecosystem: the Seregeti (Tanzania, Kenya). *Ecol. Monographs* 55: 259-94.
- MITTELBAACH, G.G. and K.L. GROSS. 1984. Experimental studies of seed predation in old-fields. *Oecologia* 65: 7-13.
- NIXON, C. M., L. P. HANSEN, P. A. BREWER, J. E. CHELSVIG, T. L. ESKER, D. ETTER, J. B. SULLIVAN, R. G. KOERKENMEIER, and P. C. MANKIN. 2001. Survival of white-tailed deer in intensively farmed areas of Illinois. *Can. J. of Zoology* 79: 581-588.
- OLFF, H. and M. E. RITCHIE. 1998. Effects of herbivores on grassland plant diversity. *TREE* 13: 261-265.

- OSTFELD, R. S. and C. D. CANHAM. 1993. Effects of meadow vole population density of tree seedling survival in old fields. *Ecology* 74: 1792-1801.
- OSTFELD, R. S., R. H. MANSON, and C. D. CANHAM. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1531-1542.
- PAKEMAN, R. J., J. ENGELN, and J. P. ATTWOOD. 1998. Rabbit endozoochory and seedbank build-up in an acidic grassland. *Plant Ecology* 145: 83-90.
- QUIMBY, D. C.. 1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. *Ecological Monographs* 21: 61-95.
- RAY, J. C.. 2000. Mesocarnivores of Northeastern North America: Status and Conservation Issues. WCS Working Papers No. 15.
- RITCHIE, M. E. and D. R. TILMAN. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* 76: 2648-2655.
- ROONEY, T. P. and D. M. WALLER. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*. 181: 165-176.
- ROSEBERRY, J. L. 1998. Landscape characteristics and spatial patterns of eastern cottontail abundance in Illinois. *Transactions of the Illinois State Academy of Science* 91: 167-178.
- RUSSELL, F. L., D. B. ZIPPIN, and N. L. FOWLER. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. *American Midland Naturalist* 146: 1-26.
- SAMSON, D. A., T. E. PHILIPPI, D. W. DAVIDSON. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos* 65:61-80.
- SCHUPP, E. W., H. J. HEATON, and J. M. GOMEZ. 1997. Lagomorphs and the dispersal of seeds into communities dominated by exotic annual weeds. *Great Basin Naturalist* 57: 253-58.
- SIROTNAK, J. M. and N. J. HUNTLY. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81: 78-87.
- SOLE, J. D. 1995. Changes in vegetation and bobwhite quail and eastern cottontail rabbit use in a converted fescue field. *Trans. of the Kentucky Academy of Science* 56: 1-8.
- SUMPTION, K. J. and J.R. FLOWERDEW. 1985. The ecological effects of the decline of rabbits (*Oryctolagus cuniculus*) due to myxomatosis. *Mammal Rev.* 15: 151-86.

- SWIHART, R. K.. 1991. Influences of *Marmota monax* on vegetation in hayfields. J. of Mammalogy 72: 791-795.
- THOMPSON, D. Q.. 1965. Food preferences of the meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. American Midland Naturalist 74: 76-86.
- TILMAN, D.. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125: 827-52.
- TREIBER, R. 1999. Phytosociology, pedology and utilisation history of dry grassland (Festuco-Brometea, Nardo-Callunetea) in the area of the upper Rhine Plane (France, Department Haut-Rhin). Tuexenia 19: 305-342.
- WALLER, D. M. and W. S. ALVERSON. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217-226.
- WATT, A.S.. 1962. The effect of excluding rabbits from Grassland A (Xerobrometum) in Breckland, 1936-1960. J. of Ecology 50: 181-198.
- WHITAKER, J. O. Jr. and R. E. MUMFORD. 1972. Ecological studies on *Reithrodontomys megalotis* in Indiana. J. of Mammalogy 53: 850-60.
- ZEDLER, P. H. and C. BLACK. 1992. Seed dispersal by a generalized herbivore: rabbits as dispersal vectors in a semiarid California vernal pool landscape. American Midland Naturalist 128:1-10.
- ZIMMERMAN, E. G.. 1965. A comparison of habitat and food of two species of *Microtus*. J of Mammalogy 46: 605-12.

Figure 1.1. Diagram of trapping grid and location of exclosures in an old field site. Traps are on a 5 m grid. Letters inside exclosures represent different treatments. Treatments were assigned at random except for F (deer exclosures), which was erected a year later than the others.



## CHAPTER 2

### THE INFLUENCE OF RABBITS (*Sylvilagus floridanus*) ON THE COMPOSITION OF SUCCESSIONAL GRASSLANDS

#### Introduction

Mammalian herbivores can influence plant communities through a variety of direct and indirect pathways (Batzli 1994). The effects of European rabbits (*Oryctolagus cuniculus*), which eat a wide variety of herbaceous and woody plants (direct effects) and also do considerable burrowing (indirect effects via soil disturbance), have long been investigated. Exclosure experiments indicate a delay of the invasion of grasslands by woody plants (Tansley and Anderson 1925) and substantial effects of rabbits on the composition of herbaceous plant communities (Watt 1962, Sumption and Flowerdew 1985, Crawley 1990). More recent studies found that rabbits can, on one hand, enhance establishment of some plant species by dispersal of seeds in fecal deposits or endozoochory (Zedler and Black 1992, Malo and Suarez 1995, 1996, Pakeman et al. 1998a, 1998b), or, on the other hand, inhibit establishment of plants because of damage that reduces seed production (Edwards and Crawley 1999). Other than Zedler and Black (1992), I found only one study on the effects of seed dispersal by lagomorphs in the United States, and it reported little influence of 4 species of lagomorphs on plant recruitment in the Great Basin (Schupp et al. 1997).

European rabbits are very common, although patchily distributed, with densities ranging from 1/ha to 55/ha (Palomares et al. 2001). Although Eastern cottontail rabbits (*Sylvilagus floridanus*) in the U.S.A. also eat a wide variety of herbaceous and woody plants, they neither burrow nor reach such high densities (maximum densities of 10/ha; Chapman et

al. 1980, Barbour and Livaitis 1993, Mankin and Warner 1999). Furthermore, changes in hunting success for *S. floridanus* indicate that Mid-western populations have declined over the past 40-50 years, which may reflect changes in the landscape and loss of optimal habitat (Preno and Labisky 1971; Sole 1995; Roseberry 1998). Thus, the influence of lagomorphs in North American grassland may be less than in Europe, and I conducted experiments to examine their effects on grasslands in the mid-western USA.

In Illinois 17.5% of land cover is classified as rural grasslands (CTAP 2001), but less than 0.1% of native prairie remains (Samson and Knopf 1994). The great majority of today's grasslands are patches of old fields, old pastures, buffer strips along agricultural fields, or maintained roadsides. Early successional change in vegetation after release of old fields from agriculture is well known for the eastern half of the United States (Bazzaz 1996, pp. 38-43). Annual and biennial herbs dominate during the first two years but are quickly replaced by perennial herbs. Rhizomatous graminoids (grasses and sedges) and forbs replace shorter-lived perennial forbs within a few years, and woody shrubs and trees slowly invade unless regular mowing (once a year during the dormant season is usually sufficient) or fire occurs. Although introduced plant species often dominate the successional sequence, these old-field grasslands do provide habitat for many native plants and mammals as well (Lin and Batzli 1995, 2001). Because of regular disturbance (mowing or fire), such grasslands will likely remain an important part of the Mid-western landscape.

I developed five a priori hypotheses concerning the role of rabbits in successional grasslands. First, endozoochory by rabbits strongly affects short-lived plants (annuals and biennials) because density of these plants depends heavily on annual recruitment and dispersal by rabbits will take seeds to new locations. Second, because short-lived plants are



more common in early succession, the impact of rabbits is greater early rather than late in the successional sequence. Third, endozoochory by rabbits leads to greater abundance of small-seeded plants in areas with access by rabbits because small seeds are less likely to be damaged during ingestion than are large seeds. Fourth, rabbit herbivory favors unpalatable forbs over palatable forbs because of the damage suffered by palatable plants. I did not expect a strong response in graminoids because of their protected meristems. Fifth, invasion of woody plants is slowed in areas with rabbits because of winter browsing. I also examined the effects of grazing on native and introduced plant species, but had no a priori hypothesis about the outcome because all species evolved with grazing by rabbits, whether in North America or in Eurasia. Although my hypotheses predict that the vegetation in areas with rabbits should contain more annual and small-seeded plants (particularly early in succession), fewer palatable forbs, and fewer woody plants, the combined effects of dispersal (positive) and damage (negative) could result in greater, lower, or unchanged species diversity depending on tolerance to damage and competitive ability of palatable species.

### **Methods**

*Study sites.* - Because I wanted to examine the effects of rabbits over the course of succession from agricultural fields to grasslands, I conducted my experiments in 3 old fields in different stages of succession. Although I chose the fields to represent different stages of succession, I recognize that some differences might reflect local conditions rather than successional stage. To minimize site differences, I chose old fields that occurred within 1 km of one another at the Ecological Research Area of the University of Illinois located 5 km northeast of Urbana, Illinois. All fields had similar soils (silt loam or silty clay loam) and drainage (flat

topography), and each was planted to alfalfa in spring after disking the remnants of the proceeding fall's crop. The early successional field was released from agriculture in the fall of 2001, the mid-successional field in fall of 1998, and the late successional field in fall of 1989. Natural colonization of the fields followed without further disturbance, except for dormant mowing of the late successional field for several years before the start of this experiment.

*Exclosure experiments.* - In each successional field, I constructed 4-m by 4-m exclosures that allowed access of various combinations of mammalian herbivores to the vegetation depending upon the size of mammal. The only treatment combinations relevant for this paper are those that allowed either access to all herbivores (controls with no fence or a false exclosure) or access to all herbivores but rabbits (no rabbits). During August to October 2001 in the mid- and late successional fields and May 2002 in the early successional field, I established 3 replicates of each treatment at randomly located plots within a 50 X 100 m grid that had 4 m between plots in each row and 8 m between plots in each column (see appendix for details).

Exclosures consisted of corrugated, galvanized steel panels driven 10 cm into the ground and extending 45 cm above the ground. I also added a strip of aluminum flashing that extended 20 cm above the top of the steel panels. The no-rabbit exclosures had solid sides except for 5-cm diameter holes drilled through the panels at 1-m intervals at ground level to allow entry by voles and mice. To test for effects of rabbits, I compared changes in vegetation within these exclosures to changes within similar false exclosures that had 2 30-cm wide gates in each side to allow access by rabbits. Although the no-rabbit exclosures would also prevent access to other sympatric small mammals, ground squirrels

(*Spermophilus tridecemlineatus*) and solitary marmots (*Marmota monax*), I never trapped or observed these species or their sign in the immediate vicinity of our experimental fields. I compared changes in vegetation within false exclosures to those on unfenced control plots to test for effects of fencing. Live trapping indicated that voles and mice occurred on all the treatment plots. Deer could access the vegetation by reaching over the sides of the exclosures or by jumping inside, which they did as evidenced by damage to plants and by fecal deposits.

Because of the need for repeated sampling of vegetation, I used a non-destructive method to compare the differences in vegetation among treatments. Vegetation grew too high for convenient point sampling, so I estimated the contribution to cover of all species of vascular plants found in 6 permanent 0.5 X 1.5-m quadrats (4.5 m total area) located within each treatment plot. I placed a 0.5 X 1.5-m light plastic frame, divided into 12 equal sections with taut string, over each quadrat to organize our observations. To obtain accurate estimates of percent cover, I recorded the number of small sections (12.5 X 12.5-cm) covered by each plant species within each quadrat (48 sections per quadrat for a total of 288 per sample) during each sampling period. To encompass changes in vegetation throughout the growing season, I sampled each spring (May), summer (July), and autumn (September) from September 2001 to September 2004 for the mid- and late successional fields and from July 2002 (two months after the first plants emerged) to May 2005 for the early successional field. I transformed the values for each species into relative cover (% of total within each sample) to analyze composition of the vegetation. Species identification and nomenclature followed Mohlenbrock (2002).

*Rabbit populations.*- To monitor activity by rabbits, I set 18 wooden live traps (18 X 22 X 76 cm) in and around each study site for 21 days during spring, summer, and fall from fall 2002 through fall 2004 (7 trap sessions). Occasionally traps malfunctioned, and, if necessary, I extended the number of trapping days to maintain a constant number of trap nights ( $\approx 375$ ) during a trap session. I discontinued baiting with apples and carrots early in the study because it only seemed to increase the frequency of opossums (*Didelphis virginiana*) in the traps. I checked traps each day and marked each captured rabbit with numbered ear tags. All animals were released at their point of capture, although some were first used in feeding trials as described below.

*Feeding trials.*- To determine the palatability of a variety of common and uncommon grassland plants to rabbits, I conducted feeding trials in 1.5-m X 1.5-m enclosures constructed in the same style as the rabbit exclosures, except that a screen was attached across the top of the flashing to prevent access by predators and escape of rabbits. Conducting the trials in the field allowed animals to forage under relatively natural conditions, ie. exposed to natural vegetation, day length, and weather. I did not conduct feeding trials during rainy or hot ( $> 30^{\circ}\text{C}$ ) weather. To prevent foraging on preferred plants not included in a trial, I removed all dicots from the enclosure, leaving a stand of dominant grasses (mainly tall fescue, *Festuca arundinacea*). A wooden box open at one end provided shelter and a shallow dish provided ad lib water for the rabbits. The methods used in this study followed the guidelines of the American Society of Mammalogists and were approved by the University of Illinois Animal Care Advisory Committee.

To maintain their natural characteristics, I carefully dug live plants from the experimental fields, placed them into plastic pots, immediately transported them to the

enclosures, buried the pots with the upper rim at ground level, and watered them. In each trial, I presented a minimum of eight plant species, a mixture of common and uncommon species, and adjusted the number and size of plants so that availability of biomass was similar. At the start of the experiment, I noted the numbers of leaves, flowers, and fruits, and the condition of each plant. A single rabbit was then placed in the enclosure and allowed to forage for 24 hrs. I used a total of 21 different rabbits for 7 feeding trials during spring, 2003-2005 and 14 trials during fall, 2002-2004. My goal was to use 5 different rabbits to test each plant species for each season, but some species only occurred during one year of the study, some were very rare in spring or fall, and some were consistently rare, so not all species appeared in the same number of trials. As a result, only 44 of 63 species found in the sampling plots were tested on  $\geq 2$  rabbits.

After each feeding trial, the damage to each plant species was scored on a scale from 0 to 4. Zero indicated that the plant appeared untouched by the animal, 1 indicated only a little consumption (<25%), 2 indicated substantial use (25-49 %), 3 indicated severe damage (50-74%), and 4 indicated nearly complete destruction (>75%). I included all damage even if uneaten material remained on the ground. To estimate the overall palatability of a plant, I used overall mean values weighted by the number of rabbits used to test each species during a season.

*Endozoochory.* - To identify the kinds and numbers of plants commonly dispersed by rabbits at our field sites, I collected 11 deposits of fecal pellets from feeding trials, which included remains from earlier meals, and found 2 deposits of pellets in the field. I stored all pellets in a refrigerator (5 °C) for at least one month to provide cold stratification before germination. I then gently crushed each set of pellets, mixed them with water, and poured the slurry evenly

across a tray of potting soil, which I placed in a greenhouse and kept moist. As seeds germinated, I transplanted each seedling into a separate plastic pot and allowed it to grow until it became identifiable.

*Statistical methods.* - To establish similarity of treatment plots at the beginning of the experiment, I first summarized vegetational data for each treatment plot before exclosures were established in 2001 (mid- and late successional fields only because the early field was not established until spring of 2002). I then compared the community composition in each field based upon the relative abundance of all species in unfenced control plots, false exclosures, and rabbit exclosures during fall of 2001. Because I could not transform relative cover to reflect a normal distribution, as indicated by nonlinear normal probability plots, I used a non-parametric equivalent of ANOVA, the Kruskal-Wallis test, for these analyses (Zar 1996, p. 198).

To test for the effects of endozoochory on plant succession, I categorized plant species as rabbit-dispersed plants if more than one viable seed occurred in the collections of fecal pellets. I then compared the relative abundances of these rabbit-dispersed plant species in the treatment plots for each sampling period (spring, summer, and fall of 2002-2004) and conducted repeated-measures ANOVA with the rabbit access as a between-plots factor and year and season as within-plots factors. Because I was interested in factor interactions, I used a balanced design ( $n = 3$  for with- and without-rabbit treatments), which meant that I used only the fenced control plots (false exclosures) for hypothesis testing. To test whether other categories of plants considered in my hypotheses responded differently to rabbit access, I sorted plants as annuals/biennials or perennials; small (<1 mg) or large seeded (>1 mg) plants; forbs, graminoids, or woody plants; highly palatable (mean palatability >2) or

unpalatable (mean palatability  $\leq 1$ ); and native or introduced species. I then tested the significance of effect of rabbits on the relative abundance of each category using repeated-measures ANOVA as above. Because I wanted to control for repeated measures but could not establish normal distributions for our response variables, I analyzed rank-transformed data (Conover 1980).

To help interpret patterns found when hypothesis testing, I examined effects of rabbits on individual species by comparing the abundance of all plant species that regularly occurred in the treatment plots (half or more of samples during a particular season) during the season in which they were most abundant. Again, I could seldom transform the values to reflect a normal distribution, so I compared treatments with and without rabbits using the non-parametric Mann-Whitney U-test for each year (Zar 1996, p.147). To increase the power of these tests, I lumped fenced and unfenced control plots for the with-rabbits treatment, thereby increasing sample size to 6, which assumed no effect of fencing. To test for fence effects, I compared the abundance of individual plant species in fenced controls (false exclosures) to that in non-fenced controls using Mann-Whitney tests for all seasons and years. The only differences that I found between fenced and unfenced controls were for 2 patchily distributed plant species. Tall fescue (*Festuca arundinacea*) consistently had greater abundance in the fenced controls in the mid-successional field ( $P = 0.050$  for all years and seasons) and wild parsnip (*Pastinaca sativa*) consistently had greater abundance in the fenced controls in late successional field ( $P = 0.050$  for all years and seasons). Because the trends in wild parsnip and fescue occurred at the beginning and remained throughout the experiment, I concluded that these differences existed a priori and did not represent fence effects.

I could not use multivariate analyses of community structure nor repeated measures MANOVA because I had relatively few samples for each treatment and each season in each field ( $n = 3$ ). Given this small sample size, to reduce type II error we set the significance level for all analyses at  $P = 0.1$ . Although multiple comparisons of treatments on different plant species may underestimate type I error, these tests were only done to help interpret results found by hypothesis testing and not simply for post-hoc analyses, so I did not adjust significance levels using Bonferroni corrections.

Finally, I considered plant community structure by analyzing species richness, evenness, and diversity in all sampling plots. I used Simpson's index of evenness (Krebs 1999, p. 449):  $E = (1/\sum p_i^2)/S$  where  $p_i$  is the proportion of cover for the  $i^{\text{th}}$  species and  $S$  is the number of species in the sample. I calculated Gini's coefficient of diversity because of low values for evenness and small sample sizes (Lande 1996):  $G = 1 - \sum p_i^2$ . I omitted the correction factor for number of individuals in the sample ( $N/N-1$ ) because my samples were always based upon cover estimated using 288 small quadrats. Linear probability plots indicated that these measures were normally distributed, so I conducted repeated-measures ANOVA as above to identify significant effects of access by rabbits.

## Results

*Rabbits and endozoochory.*- I could not estimate the absolute abundance of rabbits because I only recaptured 1 rabbit. Rather, I present the numbers caught with the same trapping effort as an index of abundance in different fields and seasons. I caught a total of 40 different rabbits (15 in the early successional field, 20 in the mid-successional field, and 5 in the late successional field). Numbers captured during a given trapping session varied from 0-8 in the



early successional field, 1-6 in the mid-successional field, and 0-2 in the late successional field. Most were captured in the fall near the end of the breeding season and after harvest of crops in nearby fields. Eliminating the 6 rabbits caught in the fall of 2002 to include only two trap sessions (2003 and 2004) for each season, we caught 20.6% (7) in spring, 14.7% (5) in summer, and 64.7% (22) in fall.

The 13 collections of fecal pellets contained from 6 to 578 pellets (a total of 1962 pellets). Twenty-two species of plants (261 individuals) germinated (Table 2-1). Of the 16 species with more than one germinating seed, 13 occurred in our sampling plots (see appendix for a complete list of germinated species). Two species of *Amaranthus* that occurred in our fields, *A. retroflexus* and *A. hybridus*, may hybridize and could not be reliably identified to species. In addition, 53 seedlings in the family Solanaceae died before positive identification to species was possible (either the smooth ground cherry *Solanum ptychantum* or the black nightshade *Physalis subglabrata*).

*Feeding trials.* - I only report results from feeding trials for the 44 plant species tested with  $\geq 2$  different rabbits (see appendix for a complete list of plants tested). Of the 33 species tested in both spring and fall, 21 were more palatable in the spring than in the fall, 2 were the same in both seasons, and 10 were more palatable in the fall (Table 2-2). Some species that received higher palatability scores in the fall were cut and left uneaten (the horseweed *Conyza canadensis*, the common milkweed *Asclepias syriaca*, and the honey locust *Gleditsia triacanthos*). Two others were common in fall but rarely encountered in spring, and, therefore, not adequately tested for spring-fall comparisons (smooth ground cherry and black nightshade).

Among graminoids, only the introduced annual grass *Setaria viridis* and the sedge *Carex cephalophora* were highly palatable (palatability score  $> 2$ ). Introduced perennial grasses and native grasses did not score high in the palatability trials, although they were not unpalatable to rabbits (average scores  $\leq 2$  and  $> 1$ , Table 2-2). Recall that *Festuca* grew in the enclosures used for the feeding trials, which may have lowered its palatability score. Of the 16 plant species with high palatability ratings, 13 were forbs, and all of the unpalatable plant species (average scores  $\leq 1.0$ ) were forbs.

*Original vegetation.* - Throughout the study, composition of the vegetation in all 3 successional fields differed greatly from each other (Fig. 2.1). At the time I established exclosures, the mid- and late-successional fields (fall 2001) differed little among treatment plots (unfenced controls, fenced controls, no rabbits), and the early successional field (spring 2002) had no emergent plants. Only 1 of 22 species tested by Kruskal-Wallis showed even marginally significant differences among treatments in the mid-successional field ( $H_{3,3}=4.500$ ,  $P=0.105$  for timothy, *Phleum pratense*); a small amount of it occurred only in the no rabbit treatment (1.0% of cover). None of the 23 plants species in the late successional field differed among treatments ( $H_{3,3}<2.500$ ,  $P \geq 0.28$  in all cases).

When rank-transformed, none of the 12 categories of plants used to test hypotheses showed significant differences among treatments by ANOVA in either the mid-successional field or the late successional field (see Appendix 1). One of the 12 categories (introduced graminoids) did show a marginally significant difference among treatments in the late successional field ( $F_{2,6}=3.375$ ,  $P=0.104$ ), with lower abundances in the fenced control (64% of cover) than in either the unfenced control or no-rabbit treatment (80% of cover in both cases), but this difference was not significant according to Bonferroni post-hoc analysis

( $P=0.130$ ). Measures of community structure for vegetation (species richness, evenness, and diversity) in the treatment plots in fall 2001 showed no significant differences (see Appendix 1).

*Tests of Hypotheses.*- I found relatively little overall effect of rabbit access on abundance of rabbit-dispersed plants. Although striking differences in the abundance of rabbit-dispersed plants occurred among seasons and years in all 3 fields, no significant differences occurred between no-rabbit and with-rabbit (control) treatments for either rabbit-dispersed plants as a whole or for separate categories of rabbit-dispersed forbs and rabbit-dispersed graminoids (RM-ANOVA,  $F_{1,4}<2.3$ ,  $P > 0.20$  in all cases). Interactions of treatments with seasons occurred in several cases, but only the treatment X season interaction in the mid-successional field was significant ( $F_{2,8}=5.193$ ,  $P = 0.036$ ). In this case, access by rabbits reduced the abundance of rabbit-dispersed forbs 3-fold during summer but not during other seasons. Even within the no-rabbit treatment, however, these forbs contributed only 1% of the vegetation.

If endozoochory strongly affected the vegetation, I expected the positive effect of rabbits to be especially clear in annual/biennial plants and in small-seeded plants. The only consistently significant effect on annual plants occurred in the mid-successional field, however (RM-ANOVA,  $F_{1,4}=6.159$ ,  $P=0.058$ ). In this case, access by rabbits on average reduced the abundance of annual plants from 3.3% to 1.4% of cover.

Consistently, significant results indicated responses of small-seeded plants to access by rabbits in both the early and late successional fields, but the trends for graminoids and forbs differed in the latter. A treatment X season interaction in the early successional field (RM-ANOVA,  $F_{1,4}= 8.000$ ,  $P=0.047$ ) indicated higher mean abundance of small-seeded

graminoids with rabbits (47%) than without rabbits (37%) during summer but not during other seasons. Similarly, in the late successional field the mean abundance of small-seeded graminoids averaged 56 % of cover without rabbits and 83% of cover with rabbits (Fig. 2.2a, RM-ANOVA,  $F_{1,4}=5.939$ ,  $P=0.071$ ). Abundance of small-seeded forbs, however, averaged 36% of cover without rabbits compared to 12% of cover with rabbits (Fig. 2.2b;  $F_{1,4}=11.029$ ,  $P=0.029$ ).

Whether rabbits regarded plants as highly palatable or unpalatable appeared to have little effect on the relative abundance of plants. One marginally significant effect of rabbits occurred on palatable graminoids in the late successional field, which only included the sedge *C. cephalophora*, and for which the mean values of cover were 0.2% with rabbits and 0.0% with no rabbits (RM-ANOVA,  $F_{1,4}=4.455$ ,  $P=0.102$ ). Unpalatable plants did not even show a marginally significant response to access by rabbits. Similarly, no significant relationship to access by rabbits appeared for woody plants, which only occurred regularly in the treatment plots of the late successional field ( $F_{1,4}=0.638$ ,  $P=0.452$ ).

Finally, I examined the relationship of rabbit access to the abundance of introduced plants, which again showed relatively little effect of rabbits. A marginally significant treatment X year interaction occurred for introduced graminoids in the mid-successional field (RM-ANOVA,  $F_{2,8}=3.087$ ,  $P=0.102$ ), which reflected 40% greater cover in the no-rabbit treatment during 2002-2003 but not during 2001. In the late successional field the mean abundance of introduced graminoids was 36% lower in the no-rabbit treatment (Fig. 2.3a, RM-ANOVA,  $F_{2,8}=12.239$ ,  $P = 0.042$ ), whereas the abundance of introduced forbs was 80% higher in the no-rabbit treatment (Fig. 2.3b, RM-ANOVA,  $F_{2,8}=18.063$ ,  $P = 0.013$ ). No significant interactions occurred in early or late succession.

*Responses of individual plant species.* - For the early successional field 17 plant species occurred in at least half the treatment plots during at least 1 season, and I conducted 32 comparisons of abundance with and without rabbits. Only 2 significant or marginally significant trends occurred. During summer of 2004 in the early successional field, velvetleaf (*Abutilon theophrasti*) had lower mean abundance without rabbits (0.9% cover) than with rabbits (3.8% cover;  $U_{3,3}=17.5$ ,  $P=0.026$ ). A similar pattern had occurred for velvetleaf during the summer of 2002 (0.0% cover without rabbits and 4.5% cover with rabbits), although the trend was not significant. In the fall of 2004 goldenrod (*Solidago canadensis*) appeared twice as abundant without rabbits (10.1% cover) as with rabbits (4.5% cover), but the significance of this effect was marginal ( $U_{3,3}=3.0$ ,  $P=0.118$ ).

For the mid-successional field 14 species occurred in at least half the treatment plots during at least 1 of the seasons, and I conducted 36 comparisons with and without rabbits. During the falls of 2002 and 2003, goldenrod again appeared to have substantially greater mean abundance without rabbits (46.9% and 68.0% cover, respectively) than with rabbits (31.5% and 46.9% of cover, respectively), but the significance was marginal ( $U_{3,3}=3.0$ ,  $P=0.121$  in both cases). In spring of 2003, alfalfa (*Medicago hispida*), like velvetleaf in the early field, had lower mean abundance without rabbits (3.2% cover) than with rabbits (9.4% cover;  $U_{3,3}=16.0$ ,  $P = 0.071$ ). By 2004 neither of these trends held (alfalfa was almost eliminated from the field), but during that spring, pennycress (*Thlaspi arvense*) had greater abundance without rabbits (4.7% cover) than with rabbits (0.7% cover;  $U_{3,3}=1.0$ ,  $P = 0.036$ ).

For the late successional field, 11 species occurred in at least half the treatment plots during at least 1 of the seasons, and I conducted 24 comparisons with and without rabbits. Each of the 3 years in the season of greatest relative abundance (summer or fall), goldenrod

again appeared to be more abundant without rabbits (29%, 28%, and 51% cover, respectively) than with rabbits (24%, 16%, and 22 % cover, respectively), and again the significance was marginal ( $U_{3,3}=3.0$ ,  $P = 0.121$  in all cases). Finally, paralleling the results for palatable graminoids, in spring of 2004, the relatively uncommon sedge (*C. cephalophora*) occurred only in treatments with rabbits (0.7% cover) and not in those without rabbits (0.0%,  $P = 0.09$ ), and, paralleling the results for introduced graminoids, by the fall of 2004, a dominant introduced grass, tall fescue, had become much more abundant in treatments with rabbits (60% cover) than without rabbits (22% cover;  $U_{3,3}=15.0$ ,  $P = 0.020$ ).

*Community structure.*- In all of the fields, richness, evenness, and diversity of plant species varied substantially with year and season, but less so with access by rabbits (Fig. 2.4). Species evenness exhibited a season X treatment interaction (RM-ANOVA,  $F_{2,8}=4.586$ ,  $P=0.047$ ) in the early successional field, lower with rabbits in the fall than in spring or summer (Fig. 2.4b). Species richness and diversity did not reveal any other effects of rabbits in this field.

Species richness appeared to respond to rabbits in the mid-successional field (RM-ANOVA,  $F_{1,4}=4.240$ ,  $P=0.109$ ), where it remained slightly higher (by 10-14%) in plots without rabbits (Fig. 2.4a). A season X treatment interaction occurred ( $F_{2,8}=7.479$ ,  $P=0.015$ ) because the effect was more pronounced in summer than in spring or fall. Species evenness and diversity did not show significant effects of treatment nor did they show any interactions of treatment with year or season ( $F<3.3$ ,  $P > 0.14$  in all cases).

Neither species richness nor evenness showed significant effects of rabbits (RM-ANOVA,  $F_{1,4}<2.7$ ,  $P > 0.18$ ) in the late successional field, but species diversity did (Fig. 2.4). Species diversity remained 10-20% higher in plots without rabbits (Fig. 2.4c; RM-

ANOVA,  $F_{1,4}=4.803$ ,  $P=0.094$ ). No significant interactions occurred between treatment and season or year ( $F_{2,8}<1.0$ ,  $P>0.20$  in both cases).

### Discussion

*Tests of hypotheses and community structure.*- Although some clear effects of rabbits occurred, my results did not compare well with those predicted by my hypotheses. Recall that I predicted that if endozoochory was important, then the abundance of small-seeded plants and annuals should be greater on plots with access by rabbits, and the effects should be greatest in the early successional field. The only results consistent with a positive effect of endozoochory were greater abundance of rabbit-dispersed forbs in the mid-successional field during summer, greater abundance of all small-seeded plants in the early successional field during summer, and greater abundance of small-seeded graminoids in the late successional field during all seasons with access by rabbits. All of these results can be discounted, however, because 1) rabbit-dispersed plants formed only 1% of the cover in plots with rabbits in the mid-successional field during summer, 2) one of the most important small seeded plants in the early successional field (the horseweed, *Conyza canadensis*) was wind-dispersed, not rabbit-dispersed, and 3) small-seeded graminoids with greater abundance in the late successional field were introduced plants, which already had greater abundance in plots with rabbits when the experiment started. Furthermore, some of the results were inconsistent with my hypotheses. In the mid-successional field, fewer annuals occurred in plots with rabbits, and in the late successional field, fewer small-seeded forbs occurred in plots with rabbits.

Of course, to disperse seeds rabbits must first consume the fruits, and it may be that damage to the plants had a greater negative effect than the positive effect of dispersal. If so, I expected to find that palatable plants, particularly forbs, would have lower abundance with access by rabbits. I found more rabbit-dispersed forbs in summers in the mid-successional field, but I also found fewer small-seeded forbs in the late successional field with rabbits. I found consistently less goldenrod (*Solidago canadensis*) in all fields on plots with access by rabbits. This species was highly palatable in spring (Table 2), early in its development, and was the dominant small-seed forb by the 3rd year in the early successional field and in all years of the later successional fields (Fig. 2.1). These results clearly implicate damage to the plants by rabbits as having a negative effect on a dominant plant, but rabbits only slowed and did not prevent goldenrod's ascent to dominance.

Several other apparent responses of plant species to rabbits appeared more idiosyncratic. Greater abundance of velvetleaf (an unpalatable annual plant with large seeds) in the early successional field in the summer of 2004 may have simply reflected the distribution of seeds during the first growing season (2002) because a similar pattern occurred then. Reduced abundance of pennycress (an unpalatable annual plant with small seeds) in the mid-successional field during spring of 2004 remains inexplicable unless it also reflects a patchy distribution of seeds. Increased abundance of alfalfa, a palatable plant with relatively large seeds, in the same field during spring of 2003 may reflect two phenomena. First, alfalfa, like perennial grasses, has been selected to respond positively to grazing, and, second, reduction of other forbs, particularly goldenrod, may have temporarily reduced competition. The eventual demise of alfalfa during succession probably reflected its relatively low stature and the increasing dominance of taller perennial grasses and goldenrod.



Increased abundance of sedge and fescue (both perennial graminoids with relatively large seeds) with rabbits in the late successional field may simply reflect their original distributions in the field. Finally, the trends for woody plants, which only occurred regularly in the late successional plots, showed no consistent results, perhaps because rabbits were least abundant in and around this field.

I did find several trends for introduced species of plants, but those for introduced graminoids were not consistent. In the mid-successional field, introduced graminoids appeared to respond negatively to rabbits, whereas in the late successional field, they appeared to respond positively. For the latter field, however, the pattern of vegetation in the treatment simply reflected their original condition. The apparent reduction of introduced forbs by activity of rabbits in the late successional field paralleled the effects on goldenrod, the dominant native forb, and indicates a general negative impact of rabbits on perennial forbs late in succession of these grasslands. Although most of the forbs in the late successional field were palatable, two species that were not palatable, wild parsnip (*Pastinaca sativa*) and Canada thistle (*Cirsium arvense*), assumed increasing importance later in succession (Fig. 2.1). That increasing importance likely reflected, at least in part, decreased competitive ability of forbs damaged by rabbits.

Although rabbits appeared to have both positive and negative effects on different components of the vegetation, their overall effects on community structure consistently appeared to be negative. Species richness declined with rabbits in the mid-successional field, species evenness declined with rabbits in the early successional field in the fall, and species diversity declined with rabbits in the late successional field. The effects were not very large, however, in the range of 10-20%.

*Other considerations.*- Year-to-year variability in plant productivity associated with weather patterns and rapid successional change in the early successional field could obscure effects of herbivory. For instance, although I detected no overall significant difference between rabbit treatments for the abundance of rabbit-dispersed species, horseweed (*C. canadensis*), an annual plant not dispersed by rabbits, strongly dominated the vegetation in this field in 2003 but not in other years (Fig. 2.1). This necessarily meant lower abundances of rabbit-dispersed species in 2003 and likely disrupted any consistent pattern.

Given the relatively low power of our experiment in any given field, as a result of a logistical trade-off between replication within fields and number of fields used, I may not have detected responses of uncommon plant species. Three species of relatively rare (always less, usually much less, than 6% cover), palatable, rabbit-dispersed plants -- 2 forbs (chickweed, *Cerastium fontanum*, black nightshade, *S. ptychanthum*) and 1 graminoid (witchgrass, *Panicum capillare*) -- only occurred in plots without rabbits (Tables 1 and 2). When combined with the general negative effects of herbivory by rabbits on forbs discussed above, this suggests that negative effects of damage generally outweighed the positive effects of seed dispersal by rabbits. This conclusion contradicts that of Malo and Suarez (1995, 1996) for European rabbits, but their studies took place in annual grassland disturbed not only by dense populations of rabbits but also by ungulates, including cattle, a situation in which contributions to the seed bank likely assume greater importance.

*Conclusions.*- Contrary to my hypotheses, endozoochory by rabbits had little effect on abundance of plants during succession of the grasslands in our fields. Consistent with my hypotheses, damage by herbivory appeared to have substantial effects by reducing the abundance of palatable forbs, which resulted in increased abundance of unpalatable forbs.

However, this effect only slowed and did not stay the march to dominance by goldenrod. Positive effects on some forbs not dispersed by rabbits may have resulted from tolerance to grazing and temporary release from competitive effects of those less tolerant. Apparent positive effects of herbivory by rabbits on graminoids reflected bias in the sampling plots established at the beginning of the study, even though treatments were selected randomly. The relatively slight negative effects of rabbits on community structure and composition in the long term suggest that lower densities of rabbits in unexploited grasslands North America have less effect than the higher densities of their European counterparts in pastures.

### Literature Cited

- BARBOUR, M. S., and J. A. LITVAITIS. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. *Oecologia* 95:321-327.
- BATZLI, G. O. 1994. Mammal-plant interactions. *Journal of Mammalogy* 75:813-815.
- BAZZAZ, F. A. 1996. Plants in changing environments. Cambridge University Press, Cambridge, United Kingdom.
- CHAPMAN, J. A., J. G. HOCKMAN, and M. M. OJEDA C. 1980. *Sylvilagus floridanus*. *Mammalian Species* 136:1-8.
- CONOVER, W. J.. 1980. Practical nonparametric statistics, 2nd edition. John Wiley and Sons, New York.
- CRAWLEY, M. J. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology* 27:803-820.
- CRITICAL TRENDS ASSESSMENT PROGRAM (CTAP). 2001. Critical trends in Illinois Ecosystems. Illinois Department of Natural Resources. Accessed at <http://dnr.state.il.us/orep/ctap2/TOC.pdf>
- EDWARDS, G. R., and M. J. CRAWLEY. 1999. Herbivores, seed banks, and seedling recruitment in a mesic grassland. *Journal of Ecology* 87:423-35.
- KREBS, C. J. 1999. Ecological methodology. 2nd ed. Benjamin/Cummings, Menlo Park, California.

- LANDE, R. 1996. Statistics and partitioning of species diversity and similarity among multiple communities. *Oikos* 76:5-13.
- LIN, Y. K., and G. O. BATZLI. 1995. Predation on voles: an experimental approach. *Journal of Mammalogy* 76:1003-1012.
- LIN, Y. K., and G. O. BATZLI. 2001. The influence of habitat quality on dispersal, demography, and dynamics of voles. *Ecological Monographs* 71: 245-275.
- MALO, J. E., and F. SUAREZ. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104:246-55.
- MALO, J. E., and F. SUAREZ. 1996. New insights into pasture diversity: the consequences of seed dispersal in herbivore dung. *Biodiversity Letters* 3:54-57.
- MANKIN, P. C., and R. E. WARNER. 1999. A regional model of the eastern cottontail and land-use changes in Illinois. *Journal of Wildlife Management* 63:956-963.
- MOHLENBROCK, R. H. 2002. Vascular flora of Illinois. Southern Illinois University Press, Carbondale and Edwardsville, Illinois.
- PAKEMAN, R. J., J. P. ATWOOD, and J. ENGELEN. 1998a. Sources of plants colonizing experimentally disturbed patches in an acidic grassland in eastern England. *Journal of Ecology* 86:1032-41.
- PAKEMAN, R. J., J. ENGELEN, and J. P. ATWOOD. 1998b. Rabbit endozoochory and seedbank build-up in an acidic grassland. *Plant Ecology* 145:83-90.
- PALOMARES, F., M. DELIBES, E. REVILLA, J. CALZADA, and J. M. FEDRIANI. 2001. Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. *Wildlife Monographs* 148:1-36.
- PRENO, W. L., and R. F. LABISKY. 1971. Abundance and harvest of doves, Pheasants, bobwhites, squirrels, and cottontails in Illinois, 1956-69. Illinois Department of Conservation Technical Bulletin Number 4:1- 76.
- ROSEBERRY, J. L. 1998. Landscape characteristics and spatial patterns of eastern cottontail abundance in Illinois. *Transactions of the Illinois State Academy of Science* 91:167-178.
- SAMSON, F. B., and F. L. KNOPF. 1994. Prairie conservation in North America. *Bioscience* 44:418- 421.

- SCHUPP, E. W., H. J. HEATON, and J. M. GOMEZ. 1997. Lagomorphs and the dispersal of seeds into communities dominated by exotic annual weeds. *Great Basin Naturalist* 57:253-258.
- SOLE, J. D. 1995. Changes in vegetation and bobwhite quail and eastern cottontail rabbit use in a converted fescue field. *Transactions of the Kentucky Academy of Science* 56:1-8.
- STANIFORTH, R. J. and P. B. CAVERS. 1977. The importance of cottontail rabbits in the dispersal of *Polygonum* species. *Journal of Applied Ecology* 14:261-7.
- SUMPTION, K. J. and J. R. FLOWERDEW. 1985. The ecological effects of the decline of rabbits (*Oryctolagus cuniculus*) due to myxomatosis. *Mammal Review* 15:151-86.
- TANSLEY, A. G., and R. S. ADAMSON. 1925. Studies of the vegetation of the English chalk. *Journal of Ecology* 13:177-223.
- WATT, A. S. 1962. The effect of excluding rabbits from Grassland A (*Xerobrometum*) in Breckland, 1936-1960. *Journal of Ecology* 50:181-198.
- ZAR, J. H.. 1996. Biostatistical analysis. Prentice-Hall.
- ZEDLER, P. H., and C. BLACK. 1992. Seed dispersal by a generalized herbivore: rabbits as dispersal vectors in a semiarid California vernal pool landscape. *American Midland Naturalist* 128:1-10.

Table 2-1. Plants germinated from fecal pellets of rabbits. Asterisks indicate species not present in sampling plots in grasslands.

Plant species	# plants germinated	% of all germinated plants
<i>Amaranthus</i> spp.	64	24.5
Solanaceae		
<i>Physalis subglabrata</i>	9	3.4
<i>Solanum carolinense</i>	7	2.7
<i>Solanum ptychanthum</i>	3	1.1
unidentified ( <i>P. s.</i> or <i>S. p.</i> )	53	20.3
<i>Ceratium fontanum</i>	24	9.1
<i>Setaria viridis</i>	19	7.3
<i>Cyperus esculentus</i> *	17	6.5
<i>Portulaca oleracea</i>	14	5.4
<i>Digitaria ischaemum</i>	13	5.0
<i>Chenopodium album</i> *	10	3.8
<i>Rumex crispus</i>	9	3.4
<i>Urtica dioica</i> *	5	1.9
<i>Panicum capillare</i>	2	<1
<i>Polygonum persicaria</i>	2	<1
<i>Elymus canadensis</i>	2	<1
<i>Barbarea vulgaris</i>	2	<1
<i>Digitaria sanguinalis</i>	1	<1
<i>Achillea millefolia</i> *	1	<1
<i>Solidago canadensis</i>	1	<1
<i>Veronica arvensis</i>	1	<1
<i>Plantago major</i>	1	<1
<i>Chamaesyce maculata</i>	1	<1

Table 2-2. Growth forms (F = forb, G = graminoid, W = woody), life history (A = annual or biennial, P = perennial), seed size (Tiny < 0.1 mg, Small 0.1-1.0 mg, Medium 1-3 mg, Large > 3.0 mg), and mean palatability scores (ranging from 0 for untouched to 4 for completely clipped) for plant species used in at least 2 rabbit feeding trials. Asterisks indicate non-native species. Woody plants tested at immature, herbaceous stage indicated by (imm).

Plant species	Growth form	Life history	Seed size	Palatability score				Weighted mean
				Spring N	Spring Mean	Fall N	Fall Mean	
<i>Viola affinis</i>	F	P	T	4	3.8	1	3.0	3.6
<i>Aster ericoides</i>	F	P	T	2	2.5	7	3.6	3.3
<i>Polygonum persicaria</i> *	F	A	M	3	3.0	5	3.4	3.3
<i>Trifolium pratense</i> *	F	P	M	5	3.4	15	3.1	3.2
<i>Medicago sativa</i> *	F	P	M	4	3.0	8	3.1	3.1
<i>Taraxacum officinale</i> *	F	P	T	5	3.6	10	2.6	2.9
<i>Setaria viridis</i> *	G	A	S	2	3.5	5	2.6	2.9
<i>Geum canadense</i>	F	P	M	4	3.3	7	2.6	2.8
<i>Rosa multiflora</i> * (imm)	W	P	S	5	3.2	7	2.3	2.7
<i>Solanum ptychanthum</i>	F	P	M	2	2.0	1	4.0	2.7
<i>Vitis palmata</i> (imm)	W	P	M	2	2.5	0	--	2.5
<i>Calystegia sepium</i>	F	P	T	5	2.4	0	--	2.4
<i>Gleditsia triacanthos</i>	W	P	L	2	2.0	9	2.4	2.4
<i>Rumex crispus</i> *	F	P	S	4	3.0	4	1.5	2.3
<i>Carex cephalophora</i>	G	P	M	4	2.5	4	2.0	2.3
<i>Physalis subglabrata</i>	F	P	M	1	0.0	4	2.8	2.2
<i>Panicum capillare</i>	G	A	T	0	--	2	2.0	2.0
<i>Sida spinosa</i> *	F	A	M	0	--	2	2.0	2.0
<i>Cerastium fontanum</i> *	F	P	T	5	2.0	0	--	2.0
<i>Festuca arundinacea</i> *	G	P	M	3	2.0	4	2.0	2.0
<i>Solidago canadensis</i>	F	P	T	5	2.6	10	1.2	1.7
<i>Ambrosia trifida</i>	F	A	L	3	2.3	5	1.2	1.6
<i>Solanum carolinense</i>	F	P	M	3	2.7	7	1.1	1.6
<i>Conyza canadensis</i>	F	A	T	3	1.3	2	2.0	1.6
<i>Bromus japonicus</i> *	G	A	M	2	2.0	2	1.0	1.5
<i>Oxalis corniculata</i> *	F	P	T	3	1.3	1	2.0	1.5
<i>Elymus canadensis</i>	G	P	L	4	1.5	5	1.2	1.3
<i>Poa pratensis</i> *	G	P	S	5	1.8	2	0.0	1.3
<i>Bromus inermis</i> *	G	P	S	5	1.4	6	1.2	1.3
<i>Cirsium arvense</i> *	F	P	T	2	3.0	6	0.7	1.3
<i>Phleum pratense</i> *	G	P	S	1	4.0	3	0.3	1.2
<i>Dactylis glomerata</i> *	G	P	S	3	1.3	11	1.2	1.2
<i>Abutilon theophrasti</i> *	F	A	L	3	0.7	2	2.0	1.2
<i>Amaranthus spp.</i> *	F	A	S	4	1.0	2	1.0	1.0
<i>Barbarea vulgaris</i> *	F	A	M	4	1.5	5	0.2	0.8
<i>Thlaspi arvense</i> *	F	A	S	4	0.8	0	--	0.8
<i>Asclepias syriaca</i>	F	P	L	2	0.0	4	0.3	0.2
<i>Pastinaca sativa</i> *	F	A	M	2	0.0	9	0.1	0.1

Figure 2.1. Mean percent of cover during September for major components of vegetation on plots ( $n = 3$ ) accessible to rabbits (Y) and not accessible to rabbits (N) in a) an early successional, b) a mid-successional, and c) a late successional old field.

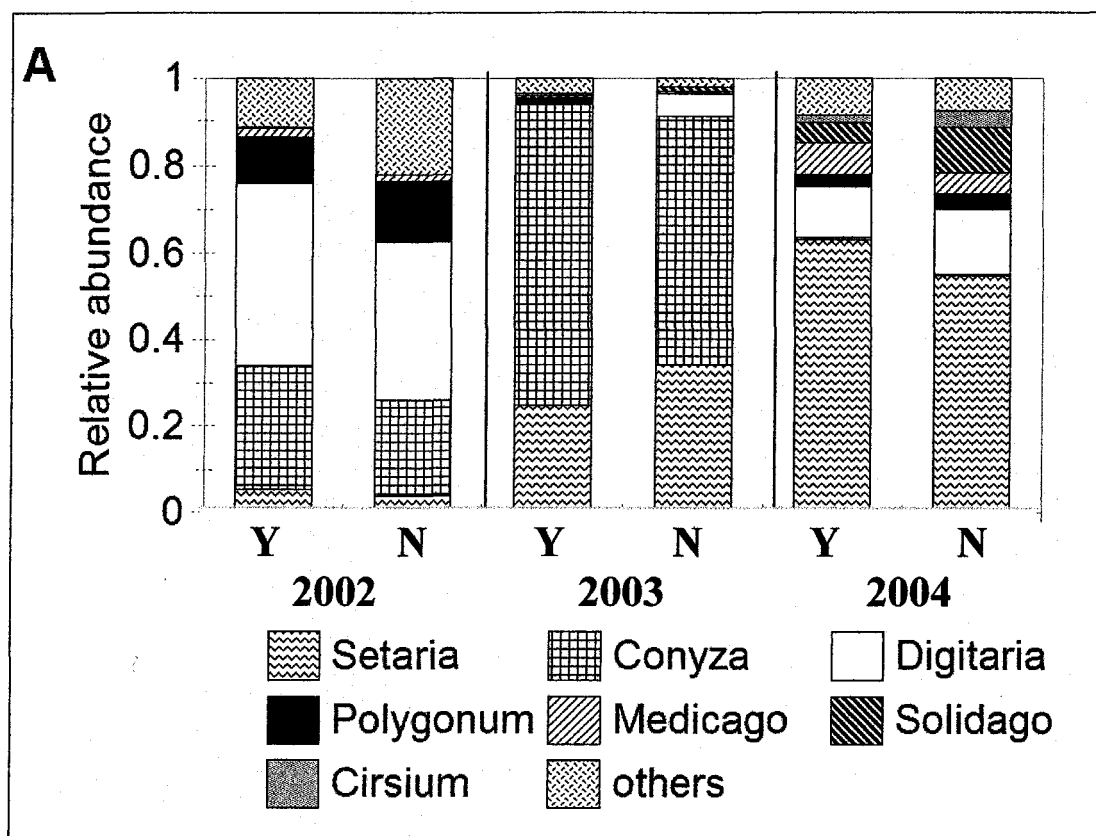




Figure 2.1. (cont.)

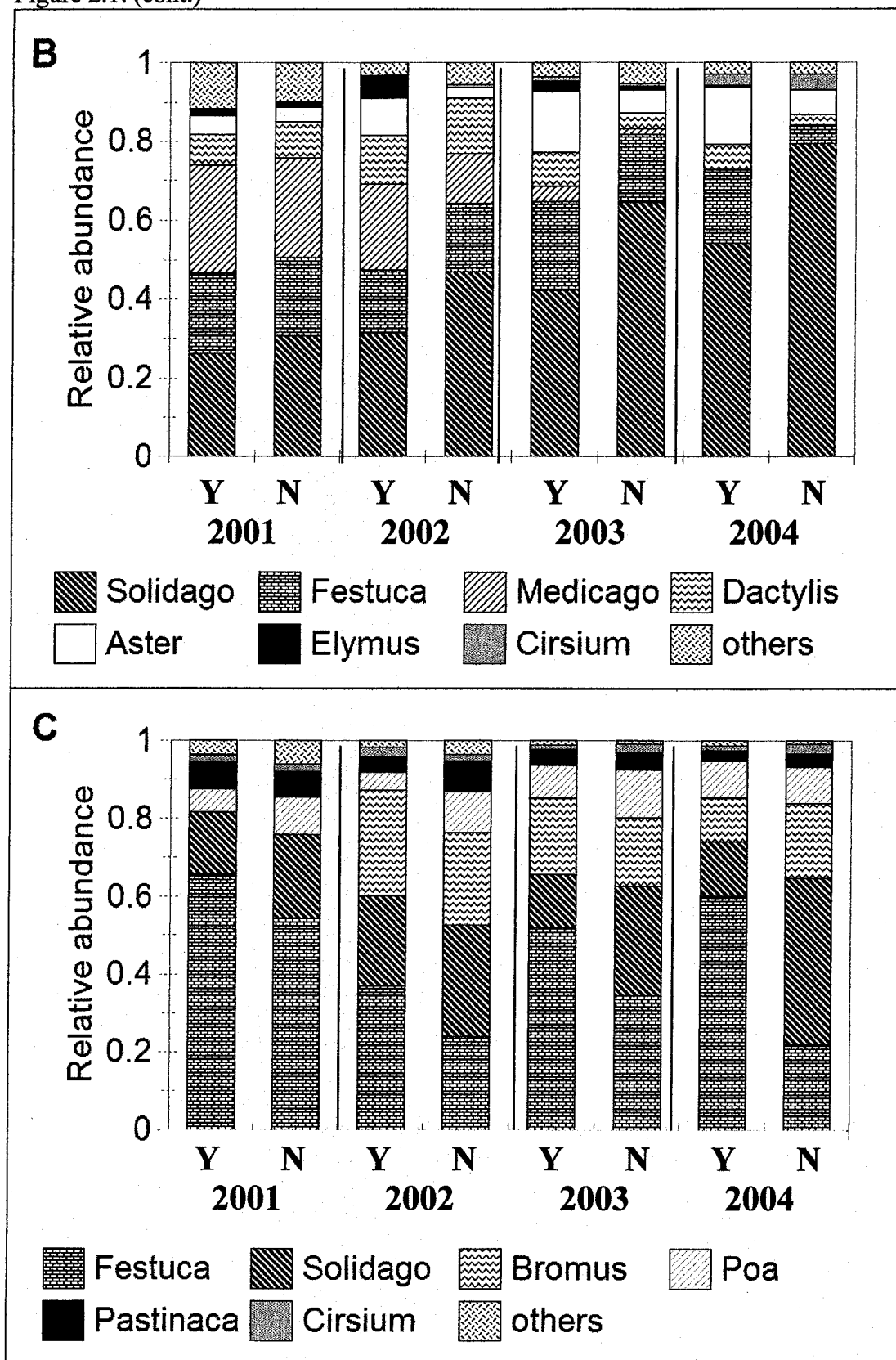


Figure 2.2. Mean ( $\pm 1 SE$ ) percent cover of a) small-seeded forbs and b) small-seeded graminoids. Means across replicates and seasons ( $n = 9$ ) for years 1-3 from an early successional field, years 5-7 from a mid-successional field, and years 14-16 from a late successional field. Grey circles represent plots with access by rabbits, and black asterisks represents plots without rabbit access.

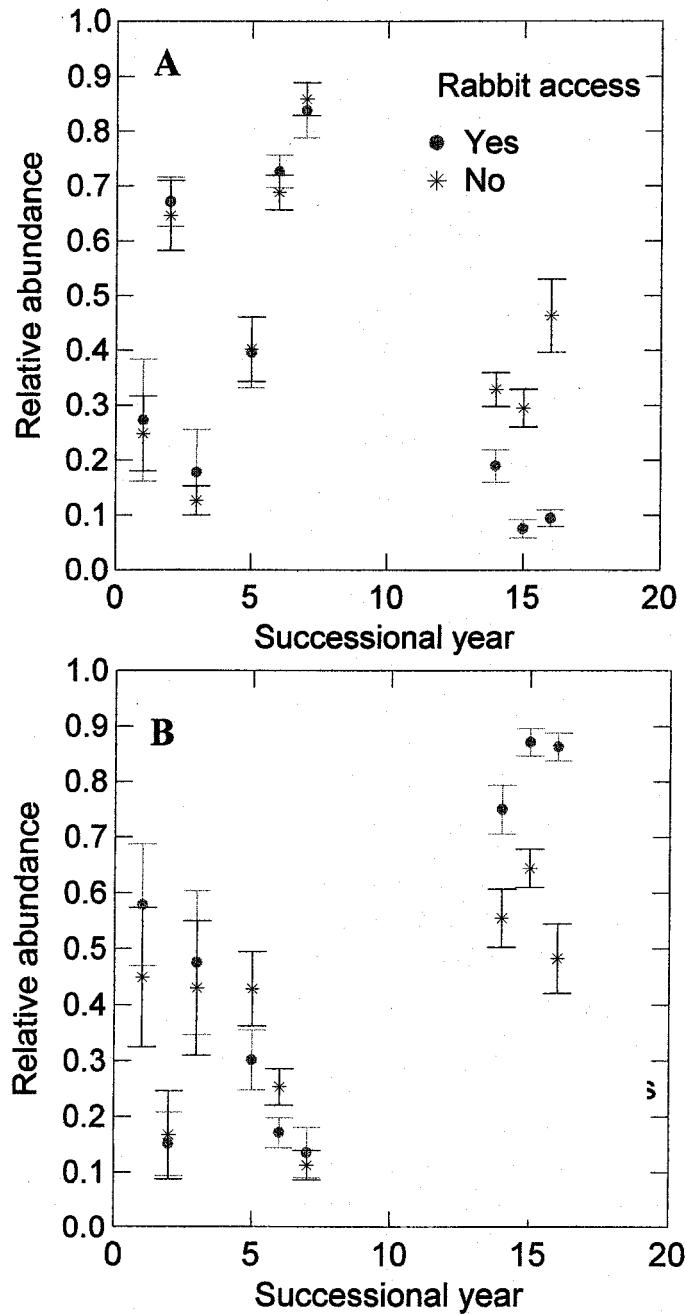


Figure 2.3. Mean ( $\pm 1 SE$ ) percent cover of a) introduced graminoids and b) introduced forbs. Symbols as in Fig. 2.2.

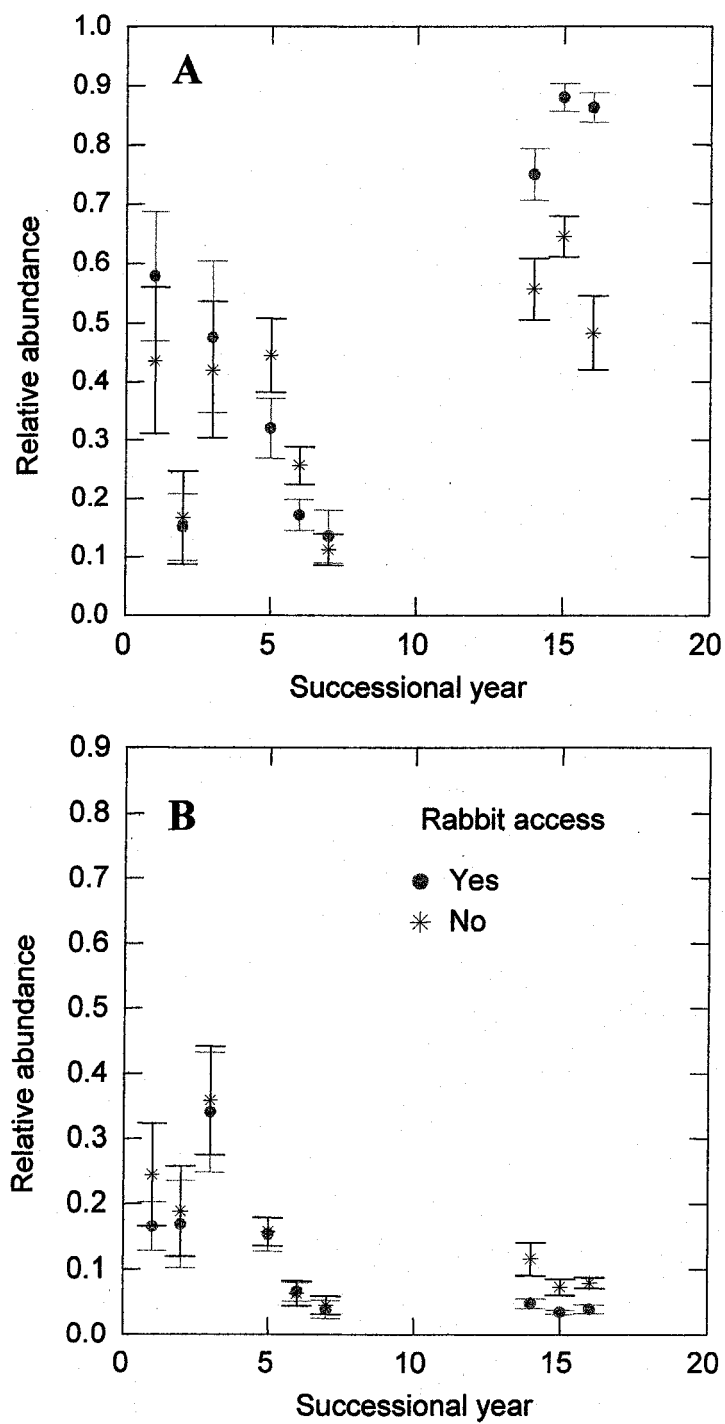
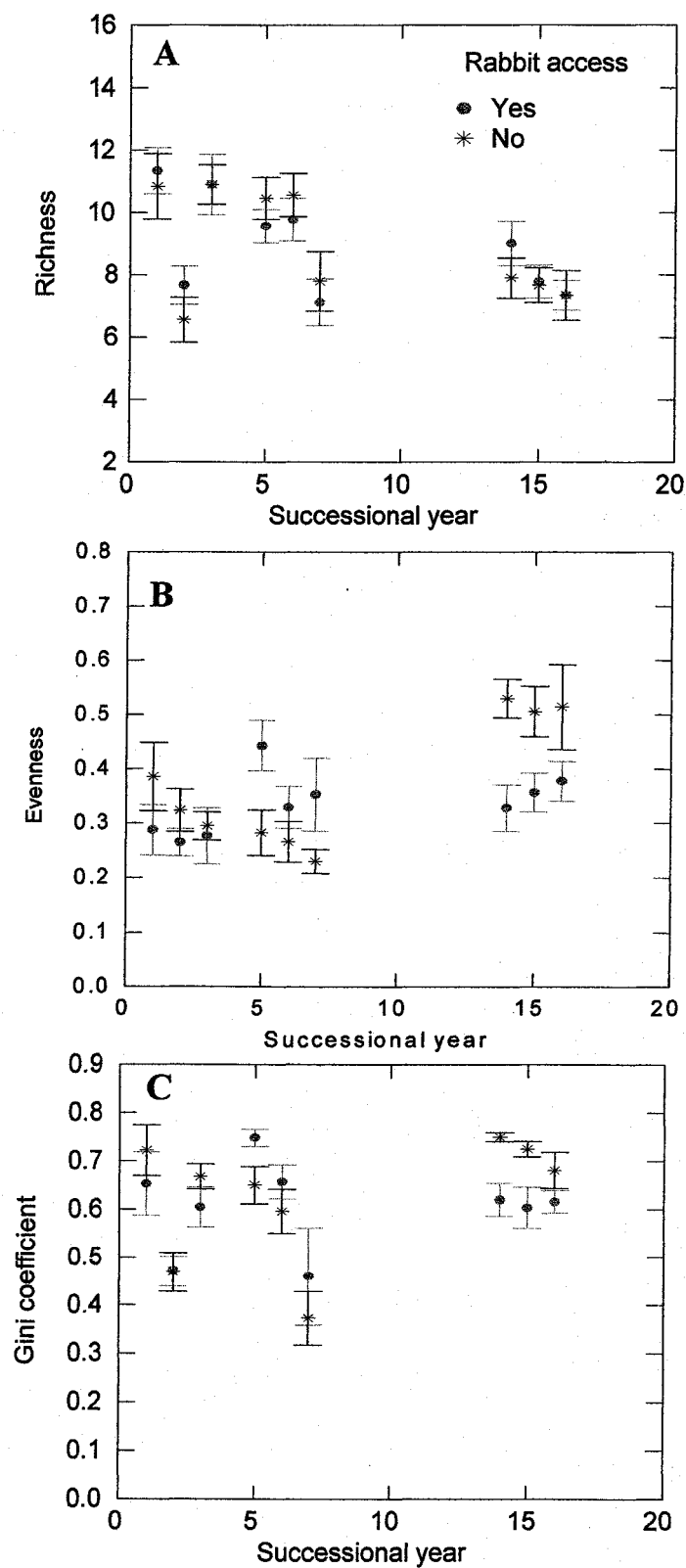


Figure 2.4. Means ( $\pm 1 SE$ ) for measures of plant community structure, including a) species richness, b) Simpson's species evenness, c) Simpson's species diversity, and d) Gini's coefficient of diversity. Symbols as in Fig. 2.2.



### CHAPTER 3

## EFFECTS OF HERBIVORY AND GRANIVORY BY MICE (*PEROMYSCUS* spp.) AND VOLES (*MICROTUS* spp.) IN SUCCESSIONAL GRASSLANDS

### Introduction

Differences in seed dispersal, growth rates, resource use, and tolerance to varying environmental conditions represent typical mechanisms commonly used to explain changes in plant community composition during succession (Connell and Slayter 1977; Tilman 1985). However, feeding patterns of herbivorous and granivorous small mammals may also directly influence development of plant communities (Huntly 1991). Herbivory on selected species can reduce species diversity by accentuating the dominance of unpalatable grass and forb species in seeded tallgrass prairie restorations (Howe and Brown 1999), whereas foraging on dominant plant species can increase plant diversity through competitive release of suppressed plant species (English and Bowers 1994, Olff and Ritchie 1998). Seed consumption can also influence plant communities. Granivorous rodents often prefer large seeds over small ones (Mittelbach and Gross 1984; Howe and Brown 2000) and studies in the Chihuahuan desert (Brown and Heske 1990, Samson et al. 1992) showed that exclusion of granivorous rodents leads to increased dominance of large-seeded plants. Thus, feeding preferences of small mammals can strongly influence the assembly of grassland plant communities.

Voles (*Microtus* spp.) eat mostly the shoots of plants, particularly monocots, although they prefer legumes (*Medicago* and *Trifolium*) and dandelions (*Taraxacum*), and also consume seeds (Thompson 1965, Zimmerman 1965, Cole and Batzli 1979, Lindroth and Batzli 1984, Marquis and Batzli 1989, Pascarella and Gaines 1991, Haken and Batzli 1996,

Sirotnak and Huntly 2000). Their diets usually consist of greater proportions of grasses than forbs because of the limited availability of preferred species. Voles forage on some annual/biennial plants in greater proportions than expected by their availability (Haken and Batzli 1996) which, because of their short life span, has strong negative effects on their abundances. Finally, by gnawing the bark of shrubs and saplings and clipping tree seedlings, high populations of voles can reduce the abundance of woody plants (Sartz 1970, Parmenter et al. 1987, Gill and Marks 1991, Hamback et al. 2004) and their invasion into grasslands (Ostfeld and Canham 1993; Ostfeld et al. 1997; Pusenius et al. 2000; Sullivan et al. 2001; Pusenius et al. 2003).

Mice (*Peromyscus spp.*) tend to be omnivorous, but their diet often consists of large proportions of a wide variety of seeds (Cogshall 1928, Whitaker and Mumford 1972, Batzli 1977, Kantak 1983). Mice and voles are major seed predators in old fields of Michigan (Mittelbach and Gross 1984) and restored prairie plantings in Illinois (Howe and Brown 1999, 2000), but the long-term effects of their activities remain unknown.

Many studies have been published on feeding habits of small mammals and their effects on desert vegetation and on tree establishment but few have examined the ways in which feeding habits of rodents affect plant communities in mid-western grasslands. Recent surveys classified 19.2% of land cover in Illinois as rural grasslands (CTAP 2001), a great majority of which are patches of old fields, old pastures, buffer strips along agricultural fields, or maintained roadsides dominated by non-native grasses. These non-native grasslands provide habitat for mice and voles (Hoffmeister 1989, Lin and Batzli 2001) and will likely remain part of the landscape.

Using exclosure experiments, I tested several hypotheses regarding the mechanisms by which mice and voles could strongly influence successional grasslands. First, voles prefer some annual plants (Haken and Batzli 1996,) which usually have few defenses against herbivory (Davidson 1993), thereby increasing the rate of disappearance of annual plants in early succession. Second, preferential consumption of large seeds by mice and voles lowers abundances of large-seeded plants in areas where these animals have access. I expected the influence of mice and voles on annual plants and germination of large-seeded plants to be more pronounced in early succession than in later successional stages because recruitment from seeds assumes greater importance early in succession. Third, damage by voles reduces the abundance of palatable forbs, which lends to an increase in unpalatable plants. I did not expect perennial graminoids to be negatively affected by herbivory because their basal meristems are less likely to be damaged by herbivory and because they rapidly regrow using nutrients stored in underground rhizomes. Fourth, voles slow the establishment of woody plants because they clip off woody seedlings and girdle saplings and shrubs. Fifth, the combination of the effects of mice and voles lowers species richness and diversity of the plant community. Overall, I expected the mice and voles to reduce the abundance of large-seeded plants, palatable forbs, and woody plants; to increase the abundance of unpalatable plants; and to lower plant diversity.

### **Methods**

*Study sites.* - I conducted my experiments in 3 old fields in different stages of succession at the Ecological Research Area of the University of Illinois located 5 km northeast of Urbana, Illinois. To minimize site differences, I chose fields that occurred within 1 km of one another

with similar soils (silt loam or silty clay loam) and drainage. All 3 fields had been planted to alfalfa in the spring following disking of the remnants of the last fall's crop. The early successional field was released from agriculture in the fall of 2001, the mid-successional field in 1998, and the late successional field in 1989. Natural colonization of the fields followed, although the late successional field was mowed once yearly during the dormant season until the start of this experiment.

*Exclosure experiments.* - In each successional field, I constructed 4-m by 4-m exclosures that allowed access of various combinations of mammalian herbivores to the vegetation depending upon the size of mammal (6 treatments in all). During August to October 2001 in the mid and late successional fields and May 2002 in the early successional field, I established 3 replicates of each treatment at random plots within a 50 X 100 m grid that had 4 m between plots in each row and 8 m between plots in each column (see Chapter 2 for details).

Exclosures consisted of corrugated, galvanized steel panels driven 10 cm into the ground and extending 45 cm above the ground. I also added a strip of aluminum flashing that extended 20 cm above the top of the steel panels to prevent mice from climbing the sides. I conducted analyses to determine the effect of fencing on plant communities (see Chapter 2) and the only differences between fenced and unfenced controls were for 2 patchily distributed plant species: tall fescue (*Festuca arundinacea*), which had consistently greater abundance in the fenced controls in mid-succession ( $P = 0.050$  for all years and seasons), and wild parsnip (*Pastinaca sativa*), which had consistently greater abundance in the fenced controls in late succession ( $P = 0.050$  for all years and seasons). The trends for both species occurred at the beginning and remained throughout the experiment, so I



concluded that these differences existed a priori and did not represent fence effects. Here, I only analyze data for the 3 of 6 treatment combinations relevant for this paper: 1) no-access, which used exclosures to exclude all rodents and lagomorphs, 2) mouse-only access (m-plots) had 1.3-cm diameter holes drilled through the panels at ground level in 1-m intervals to allow mice to enter and 3) mouse and vole access (m+v plots) had 4.4-cm diameter holes drilled through the panels at ground level in 1-m intervals to allow mice and voles to enter. The effects of each mammal type would then be calculated by the difference between the treatments with and without that type of animal. The difference between the no-access and the m-plots would show the effect of mice while the difference between the m-plots and the m+v plots would show the effect of voles.

I set 4 Sherman traps inside each exclosure for a period of one week upon completion of exclosures to remove animals inside prohibited areas. Subsequently, to check that no mice or voles occurred inside the no-access plots and that they did visit the accessible exclosures, I regularly trapped inside exclosures when assessing mouse and vole populations on the study sites (see below). Deer could access the vegetation by reaching over the sides of the exclosures or by jumping in, which they did as evidenced by damage to plants and by fecal deposits.

Because of the need for repeated sampling of vegetation, I used a non-destructive method to compare the differences in vegetation among treatments. Vegetation grew too high for convenient point sampling, so I estimated the contribution to cover of all species of vascular plants in 6 permanent 0.5 X 1.5-m quadrats (4.5 m total area) within each treatment plot. I placed a 0.5 X 1.5-m rigid plastic frame, divided into 12 equal sections with taut string, over each quadrat to organize our observations. To obtain accurate estimates of

percent cover, I recorded the number of small sections (12.5 X 12.5-cm) covered by each plant species within each quadrat (48 sections per quadrat for a total of 288 per sample) during each sampling period. To encompass changes in vegetation throughout the growing season, I sampled each spring (May), summer (July), and autumn (September) from September 2001 through May 2005 for the mid- and late successional fields and from July 2002 (two months after the first plants emerged) through May 2005 for the early successional field. Because absolute cover estimates varied among seasons and years and could exceed 100%, I transformed the values for each species into relative cover (% of total within each sample for each treatment) to analyze composition of the vegetation. Species identification and nomenclature followed Mohlenbrock (2002).

*Rodent populations.*- To document the use of the study sites by small mammals, I conducted live-trapping every May, July, and September from May 2002 through September 2004. I set one Sherman trap baited with sunflower seeds at each of 105 stations 5 meters apart on a grid of 7 by 15 in each grassland. I set traps for 4 consecutive nights in each field and checked them every morning and evening. I attached a numbered eartag to each animal and released them at the point of capture, although some were first used in feeding trials as described below.

*Feeding trials.*- To determine the palatability of common and uncommon grassland plants to mice and voles, I conducted feeding trials in 1.5-m X 1.5-m enclosures constructed in the same style as the exclosures, except that I attached a screen across the top of the flashing to prevent access by predators. Conducting the trials in the field allowed animals to forage under relatively natural conditions, ie., exposed to natural vegetation, day length, and weather. To prevent foraging on preferred plants not included in the trial, I removed all

dicots from the enclosure, leaving only dominant grasses (mainly *Bromus inermis* and *Festuca arundinacea*). A wooden nest box with cotton bedding provided shelter and a shallow dish provided ad lib water for the rodents.

To maintain their natural characteristics, I carefully dug live plants from the experimental fields, placed them into plastic pots, immediately transported them to the enclosures, buried the pots with the upper rim at ground level, and watered them. In each trial, I presented 5 to 10 plant species, a mixture of common and uncommon species, and adjusted the number and size of plants so that availability of biomass was similar. At the start of the experiment, I noted the numbers of leaves, flowers, and fruits, and the condition of each plant. Then I placed a single rodent in the enclosure and allowed it to forage for 24 hrs. I used a total of 196 different rodents for feeding trials from spring 2003 through spring 2005. My goal was to use 5 different animals of each of the 3 common rodent species (*Peromyscus leucopus*, *Microtus ochrogaster*, and *M. pennsylvanicus*) to test palatability of each plant species in each of the 3 seasons, but some plant species only occurred during 1 year of the study, some were very rare in some seasons, and some were consistently rare, so not all species appeared in the same number of trials. Since I caught only 1 *M. pennsylvanicus* in the early successional grassland during this study, I only tested plant species present in the mid- and late successional grasslands with this species.

In addition to testing the palatability of plant shoots, I tested palatability of seeds to the mammals by providing seeds from 3 additional plant species in each feeding trial during the season in which the seeds matured in the field. I collected seeds from plants in the surrounding grassland, dried them in the lab, and pre-weighed them into 1-2 gram rations. I placed seeds of each species into shallow dishes and placed 15 x 30 cm corrugated metal

panels 10 cm above the dishes to prevent the seeds from being washed out by rain. I conducted granivory feeding trials with 26 relatively common plant species. I did not use species with extremely small seeds ( $<0.1$  mg), such as *Aster ericoides*, *Cerastium fontanum*, and *Solidago canadensis*, or species that were rarely encountered in the grassland. My goal was to use 5 different animals of each species with each type of seed, but for some plant species I was unable to collect enough seeds, so not all species appeared in the same number of trials. I conducted more than 5 trials with many species of seed for *P. leucopus* to ensure that the mice had enough food available.

After each feeding trial, I scored damage to each plant species on a scale from 0 to 4. Zero indicated that the plant appeared untouched by the animal, 1 indicated slight damage ( $<25\%$ ), 2 indicated moderate damage (25-49 %), 3 indicated severe damage (50-74%), and 4 indicated nearly complete destruction ( $>75\%$ ). I included all damage even if uneaten material remained on the ground because the impact on the plant did not depend on consumption. To estimate the overall palatability of a plant to each mammal species, I weighted mean values across seasons by the number of animals used for tests of the plant species during a season. To assess seed palatability, I took the remaining seeds to the lab where they were dried and re-weighed to determine the difference between initial weights and final weights.

*Statistical methods.* - To establish similarity of treatment plots in the mid- and late successional fields at the beginning of the experiment, I compared the community composition based upon the relative abundance of each species before establishing the exclosures (Fall 2001). Because probability plots indicated that efforts to transform relative cover to reflect normal distributions failed, I used a non-parametric equivalent of ANOVA,

the Kruskal-Wallis test, for these analyses (Zar 1996, p. 198). I also compared the abundances of plants in the categories used to test my hypotheses and the values for measures of community structure (richness, evenness, and overall diversity—see details below). Because these two sets of data were normally-distributed, I used a one-way ANOVA to test for differences among the treatment groups. I could not compare the initial vegetation in sampling plots for the early successional field because there was no emergent vegetation in Spring 2002 when the exclosures were first established.

I calculated Pearson's correlation coefficient to identify the relationship between seed size and mean weights of species of seeds consumed by each mammal species. I considered seeds with weights  $< 1.5$  mg small and those  $> 1.5$  mg large (following Howe and Brown 1999), which almost evenly divided the plant species into the two categories. Using mean values of consumption for each species of seeds, I conducted a one-way ANOVA to determine if the 3 mammal species differed from one another in their overall consumption of seeds. To determine if any of the 3 mammal species preferred large seeds over small ones, I log-transformed the mean weight of consumed seeds of each plant species to normalize distributions and conducted a t-test for each mammal species.

To test my hypotheses, I categorized plants as small- ( $< 1.5$  mg) or large-seeded ( $> 1.5$  mg); highly palatable (mean palatability  $> 2$  for at least one mammal species) or unpalatable foliage (mean palatability  $\leq 1$  for all mammal species); plants with palatable seeds (mean consumption of  $> 250$  mg by at least one species); annuals/biennials or perennials; and forbs, graminoids, or woody plants. I then conducted repeated-measures ANOVA with access (no-access, m-plots, m+v plots) as a between-plots factor and year and season as within-plots factors on the relative abundance of each category for each successional old field. For the

repeated-measures analyses, I used 3 years of data with 3 seasons in each year. I wanted to control for repeated measures but frequently could not establish normal distributions for the response variables. I, therefore, conducted analyses with rank-transformed data (Conover 1980). For the mid- and late successional fields, however, the number of sampling periods in the graphs presented also include data from fall 2001 and spring 2005.

To help interpret patterns found when hypothesis testing, I examined effects of rodents on individual species by comparing the abundance of all plant species that regularly occurred in our treatment plots (at least 2 of 3 replicate plots for at least one treatment) during the season in which they were most abundant. I could seldom transform the values to reflect a normal distribution, so I compared treatments for each year using the non-parametric Kruskal-Wallis test. Although multiple comparisons of treatments on different plant species may lead to underestimates of type I error, these tests were only done to help interpret results found by hypothesis testing. Therefore, I did not adjust significance levels using Bonferroni corrections. I could not use multivariate analyses of community composition nor repeated measures MANOVA because I had too few replicates for each treatment ( $n = 3$ ).

Finally, I considered plant community structure by analyzing species richness, evenness, and diversity in all plots. I used Simpson's index of evenness (Krebs 1999, p. 449):  $E = (1/\sum p_i^2)/S$  where  $p_i$  is the proportion of cover for the  $i^{\text{th}}$  species and  $S$  is the number of species in the sample. I used Gini's coefficient of diversity for an unbiased index of diversity given low values for evenness and small sample sizes (Lande 1996):  $G = 1 - \sum p_i^2$ . I omitted the correction factor for number of individuals in each sample ( $N/N-1$ ) because my samples were based upon cover estimated in 288 small quadrats. Linear probability plots

indicated that these measures were normally distributed, so I conducted repeated-measures ANOVA as above to identify significant effects of access by rodents.

Throughout this study, given my small sample size ( $n=3$ ), I set the significance level for all analyses at  $P = 0.1$  to reduce type II error and expected to detect only fairly large effects.

## Results

*Rodent populations.*- Granivores dominated the rodent community of the early successional grassland. In addition to the most abundant rodent, *Peromyscus leucopus* (60% of 185 individuals captured; Fig. 3.1), I also caught *Microtus ochrogaster* (14%), *P. maniculatus* (10%), *Reithrodontomys megalotis* (9%), *Zapus hudsonius* (6%), and *M. pennsylvanicus* (<1%). I never caught *P. maniculatus* in the mid- or late successional grasslands, although I did catch the other mice there. Herbivores dominated the rodent communities in the mid- and late successional fields: 126 *M. pennsylvanicus* among the 235 individuals (59%) captured in mid-succession and 103 among the 168 individuals (62%) in late succession; 26 *M. ochrogaster* in mid-succession and 18 in late succession, 12% of the individuals in both fields.

Throughout my 3 years of trapping, in the early successional grassland I caught 7 mice (1 *P. maniculatus*, 2 *R. megalotis*, and 4 *P. leucopus*) inside the m-plots, and 10 mice (1 *Z. hudsonius*, 1 *P. maniculatus*, 2 *R. megalotis*, and 6 *P. leucopus*) and 2 voles (*M. ochrogaster*) inside the m+v plots. In the mid-successional grassland, I caught 6 mice (all *P. leucopus*) and 3 juvenile voles (*M. pennsylvanicus*) inside the m-plots, and 5 mice (1 *R. megalotis* and 4 *P. leucopus*) and 18 voles (3 *M. ochrogaster* and 15 *M. pennsylvanicus*)

inside the m+v plots. In the late successional field, I caught 3 mice (all *P. leucopus*) inside the m-plots and 16 voles (3 *M. ochrogaster* and 13 *M. pennsylvanicus*) inside the m+v plots. These numbers roughly reflected the relative densities of rodents in the unexclosed areas of the grassland. I never caught any mice or voles inside the no-access plots.

*Feeding trials.*- Of 26 plant species that I tested with *M. pennsylvanicus*, 5 were highly palatable (mean palatability scores >2.0; Table 1): a biennial legume (*Trifolium pratense*), a perennial legume (*Medicago sativa*), a perennial dicot (*Taraxacum officinale*), and 2 perennial grasses (*Bromus inermis* and *Festuca arundinacea*). Fifteen species were unpalatable (mean palatability scores  $\leq 1.0$ ), 5 of which were annual/biennial. Only 1 annual plant, *Bromus japonicus* (Japanese brome), was moderately palatable to *M. pennsylvanicus*. Palatability scores of 41 plant species (15 annual/biennial) tested with *M. ochrogaster* showed only 3 dicots, the same as for *M. pennsylvanicus*, (*T. pratense*, *M. sativa*, *T. officinale*) and 1 perennial grass (*Lolium perenne*) as highly palatable. Of the 30 unpalatable species, 12 were annual or biennial. The two remaining annual/biennials (*B. japonicus* and *Ambrosia trifida*) were moderately palatable to *M. ochrogaster*. I tested *P. leucopus* with the same 41 plant species as *M. ochrogaster*, but the mice found no species highly palatable. In fact, only three species were even moderately palatable to the mice: two annual forbs (*Barbarea vulgaris* and *Abutilon theophrasti*) and one annual grass (*Echinochloa crus-galli*).

Pearson's correlation coefficient ( $r$ ) indicated a significant positive relationship between seed size and consumption for *P. leucopus* ( $r = 0.62$ ,  $P=0.002$ ), but not for *M. ochrogaster* ( $r = -0.05$ ,  $P=0.823$ ) or *M. pennsylvanicus* ( $r = -0.13$ ,  $P=0.620$ ). Although there was a trend for *Peromyscus* to consume more seeds than either vole species ( $0 \pm \text{SE} = 0.33 \text{ g} \pm 0.7$  for *P. leucopus*,  $0.16 \text{ g} \pm 0.5$  for *M. ochrogaster*, and  $0.23 \text{ g} \pm 0.7$  for *M.*



*pennsylvanicus*), there was no statistically significant difference among the three (one-way ANOVA,  $F_{2,59}=1.698$ ,  $P=0.140$ ). However, because the mean size of *Peromyscus* in our feeding trials was 22 g, whereas the mean of *Microtus* was 42 g, *Peromyscus* did consume more seeds on a per gram body weight basis. When seeds were grouped into large (>1.5 mg) and small (<1.5 mg) for mean consumption by rodents, I found no difference in the amount of large or small seeds consumed ( $0 \pm \text{SE} = 0.28 \text{ g} \pm 0.06$  for large,  $0.22 \text{ g} \pm 0.05$  for small; t-test, t-stat=0.794, d.f.=60,  $P=0.430$ ). When I analyzed consumption of seeds for each mammal species separately, I found that *P. leucopus* had a greater tendency to take more large seeds than small ( $0 \pm \text{SE} = 0.43 \text{ g} \pm 0.12$  for large seeds,  $0.26 \text{ g} \pm 0.08$  for small; t-stat=1.270, df=21,  $P=0.218$ ), but no species showed a significant preference (*M. ochrogaster*  $0 \pm \text{SE} = 0.23 \text{ g} \pm 0.08$  for large,  $0.16 \text{ g} \pm 0.06$  for small, t-stat=0.716, df=20,  $P=0.482$ ; *M. pennsylvanicus*  $0 \pm \text{SE} = 0.15 \text{ g} \pm 0.07$  for large,  $0.26 \text{ g} \pm 0.10$  for small, t-stat=-0.858, df=18,  $P=0.404$ ).

As seen in Table 3-2, some large seeds were not heavily consumed by mice or voles (<150 mg/24 hrs; *Lolium perenne*, *Barbarea vulgaris*, and *Asclepias syriaca*) and some small seeds were (>600 mg/24 hrs; *Setaria viridis*, *Phleum pratense*, *Pastinaca sativa*). The different mammalian species did prefer somewhat different species of seeds. On average, *P. leucopus* heavily consumed (>500 mg/24 hrs) seeds of 7 species: *Setaria viridis* (annual grass), *Elymus canadensis* and *Phleum pratense* (perennial grasses), *Abutilon theophrasti* and *Ambrosia trifida* (annual forbs), *Pastinaca sativa* (biennial forb), and *Sida spinosa* (perennial forb); *M. pennsylvanicus* heavily consumed seeds of 4 species (*E. canadensis*, *P. pratense*, *P. sativa* and *Carex cephalophora*, a perennial sedge) and *M. ochrogaster* heavily consumed 3 species (*E. canadensis*, *S. spinosa*, and *S. viridis*).

*Original vegetation.* - I found no significant differences among our three treatment levels (no-access, m-access, m+v access) at the time the exclosures were established in the mid- and late-successional fields (Fall 2001). The early successional field (Spring 2002) had no emergent plants when I established the exclosures. The dominant plant species in both mid- and late succession were *Festuca arundinacea* (mean cover 20% and 59%, respectively) and *Solidago canadensis* (mean cover 33% and 23%, respectively). In addition, the mid-successional field had an mean cover of 23% *Medicago sativa*. Kruskal-Wallis tests revealed no significant differences among treatments for abundances of any plant species in the mid- or late successional fields ( $H_{3,3} < 3.0$ ,  $P > 0.20$  in all cases). None of the categories of plants used to test my hypotheses (annuals, large-seeded plants, plants with palatable seeds, palatable plants, unpalatable plants, and woody plants) showed significant differences among treatments in the mid- or late successional fields (one-way ANOVA,  $F_{2,6} < 2.5$ ,  $P > 0.29$  in all cases). Neither did significant differences occur in species richness, evenness, or diversity among treatment levels in either the mid- or late successional grasslands (one-way ANOVA,  $F_{2,6} < 2.5$ ,  $P \geq 0.225$  in all cases).

*Hypothesis testing.* - In reporting the results of data analyses for hypothesis testing, I refer to effects due to access by rodents (no-access, m-plots, and m+v plots) as treatment effects. For functional groups that are not normally distributed, I report  $P$ -values for analyses the rank-transformed data. I do not report significance of the factors of season or year because such effects are common as vegetation changes through both the course of the year and the process of succession. Likewise, to streamline the results, I do not report interaction effects unless the interactions are statistically significant ( $P \leq 0.100$ ) or almost so.

Experimental treatments did not significantly affect the abundance of short-lived plants (annual or biennial) in any field (RM-ANOVA;  $F_{1,4} < 2.5$ ,  $P > 0.29$  for all fields). Large-seeded plants in the early successional field showed significantly greater abundance in the m+v plots than in the m-plots or no-access plots in 2004 (RM-ANOVA,  $F_{2,6} = 3.838$ ,  $P = 0.084$  rt). In mid-succession, abundances of large-seeded plants did not differ with treatments (RM-ANOVA,  $F_{2,6} = 0.930$ ,  $P = 0.507$  un, 0.445 rt). Patterns in late succession resembled those in early succession, with greater abundances of large-seeded plants in the m+v plots than in the m-plots or no-access plots in 2004 (RM-ANOVA,  $F_{2,6} = 4.175$ ,  $P = 0.072$ ).

Feeding trials indicated that rodents at my sites did not dramatically discriminate among seeds based on size, and even plants with highly palatable seeds were equally abundant among treatments in early succession (RM-ANOVA,  $F_{2,6} = 0.258$ ,  $P = 0.781$ ). Significant but opposite patterns in abundance of plants with palatable seeds due to treatment occurred in mid- and late successional grasslands (RM-ANOVA,  $F_{2,6} = 21.407$ ,  $P = 0.002$  for mid-succession and  $F_{2,6} = 5.643$ ,  $P = 0.042$  for late succession). In mid-succession, the no-access plots had greater abundances of plants with palatable seeds overall than the m-plots or m+v plots (mean cover of 22, 12, and 10%, respectively; Fig. 3.2a), although there was a spike in abundance of palatable-seeded plants in spring 2005 in the plots to which rodents had access. In late succession, significantly higher abundances of plants with palatable seeds occurred in the m+v plots than the no-access plots by September 2002 (mean cover of 18 and 4%, respectively), while the m-plots had intermediate abundances ( $P = 0.070$ ; Fig. 3.2b). This pattern continued through fall 2004, at which time abundances were significantly greater in

the m+v plots than in either the m-plots or the no-access (mean cover 13%, 4% and 1%, respectively;  $P=0.002$ ).

The abundance of palatable forbs did not differ with treatment in either early or late succession (RM-ANOVA,  $F_{2,6}=0.563$ ,  $P=0.597$  for early succession and  $F_{2,6}=2.141$ ,  $P=0.199$  for late succession). However, in mid-succession, a consistent and significant trend occurred with more palatable forbs in areas without rodent access than with rodent access (RM-ANOVA,  $F_{2,6}=14.791$ ,  $P=0.005$ ; Fig. 3.3a). Analyses showed no significant interactions ( $F<0.5$ ,  $P>0.85$  for all interactions).

Palatable graminoids did not occur in sufficient abundance for analysis in early succession. Unexpectedly, however, I found significant overall effects of rodent access on palatable graminoids in both mid- and late succession (RM-ANOVA,  $F_{2,6}=3.790$ ,  $P=0.086$  for mid-succession and  $P=0.015$  for late succession; Fig. 3.3b-c). Differences between the no access and rodent-accessible plots appeared to increase over time, with more palatable graminoids (combined abundances of *Bromus inermis*, *Dactylis glomerata*, *Festuca arundinacea*, and *Lolium perenne*) in areas without rodent access. Analyses did not indicate any significant interactions in mid- or late succession ( $F<1.5$ ,  $P>0.70$  for all).

Unpalatable plants showed no differences in abundance among treatments in the early successional grassland (RM-ANOVA,  $F_{2,6}=0.042$ ,  $P=0.949$ ). In the mid-successional grassland, mean abundance of unpalatable plants ranged from 31-36% in all treatments during fall 2001, but there was a significant access X year interaction during the next three years as abundances dramatically increased in treatments with rodent access (RM-ANOVA,  $F_{2,4}=2.823$ ,  $P=0.079$ ). Mean abundances reached 80-90% in plots with rodent access but remained below 50% without rodent access (Fig. 3.4a). A similar pattern occurred in late

succession, with initial abundances of 31-41%, unpalatable plants decreasing in abundance over time in no-access plots to 10-20%, and increasing over time to 60-70% in m-access and m+v access plots (RM-ANOVA,  $F_{2,6}=7.676$ ,  $P=0.023$ ; Fig. 3.4b). There was no significant access X year interaction, however ( $P=0.936$ ).

Woody plants (tree seedlings) occurred sporadically in all three fields and were only common enough for statistical analysis in late succession and in the last 2 years of early succession. In neither field did rodent access affect abundances of woody seedlings (RM-ANOVA,  $F_{2,6}=0.115$ ,  $P=0.893$  for early succession, and  $F_{2,6}=0.474$ ,  $P=0.644$  for late succession).

*Community structure.* - I found no overall treatment effect nor any significant interactions in species richness, evenness, or diversity in early succession (RM-ANOVA,  $F_{2,6}<0.4$ ,  $P\geq 0.720$  in all cases). Species richness also did not respond to treatments in mid- or late succession (RM-ANOVA,  $F_{2,6}=P=0.791$ ,  $0.959$  respectively), although I did find a significant 3-way interaction in mid-succession ( $F_{8,24}=2.302$ ,  $P=0.055$ ), in which treatment effects during all seasons varied among years and a treatment X year interaction in late succession, with lower richness in m-plots than in no-access in 2003 and the opposite pattern by the end of 2004 ( $F_{4,12}=4.037$ ,  $P=0.029$ ).

In the mid-successional grassland, no-access plots had significantly higher species evenness than either the m-plots or m+v plots, which differed little (RM-ANOVA,  $F_{2,6}=87.856$ ,  $P<0.001$ ; Fig. 3.5a). The trends found in late succession were opposite of those in mid-succession, with highest evenness in m+v plots and lowest in no-access plots, but these differences existed in the original vegetation and changed little after the course of the experiment (RM-ANOVA,  $F_{2,6}=2.205$ ,  $P=0.191$ ; Figure 3.5b).

In mid-succession, no-access plots had significantly higher diversity than m-plots or m+v plots (RM-ANOVA,  $F_{2,6}=14.474$ ,  $P=0.005$ ; Fig. 3.5c) and there was a significant interaction between access and year ( $F_{4,12}=5.513$ ,  $P=0.009$ ), with greater differences between the no-access and rodent-access plots in later years. In the late successional grassland, I found no overall response of diversity to rodent access (RM-ANOVA,  $F_{2,6}=1.671$ ,  $P=0.265$ ) although I did find an interaction between access and season ( $F_{4,12}=4.109$ ,  $P=0.025$ ), with greater diversity with access in spring (May) and fall (September) than in summer (July).

### Discussion

*Tests of hypotheses.*- Mice and voles clearly affect the composition of the plant communities in old fields, although not in all the ways I had expected. I expected annual and biennial plants to be palatable to voles and abundances of these plants to be lower in areas with vole access. In my feeding trials, however, the only highly palatable short-lived plant was the leguminous *Trifolium pratense*. Both vole species also found *Bromus japonicus* moderately palatable and *M. ochrogaster* found *Ambrosia trifida* moderately palatable. Overall, most of the annual and biennial plants remained uneaten, which probably explains why the overall abundance of annual/ biennial plants did not differ among treatment levels.

I had expected *Peromyscus* to consume a greater amount of seeds than either species of *Microtus*. While I did find a trend for *Peromyscus* to consume more seeds than either vole species, the difference only became significant if considered per gram body mass. I also expected mice and voles to preferentially feed on large seeds (Mittlebach and Gross 1984, Howe and Brown 1999), leading to reduced abundances of large-seeded plants in areas accessible to rodents. Unlike Howe and Brown (1999), I found no change in the abundance

of large-seeded plants attributable to rodent access. Again, this probably reflected the lack of distinct preference by rodents for seeds in the larger category in my feeding trials. Numerous studies have reported significant negative influences of mouse granivory on very large seeds (eg., acorns) of plants in forests (Davidson 1993), but there were no seeds in my grasslands comparable to those.

My final expectation with regard to granivory was to find lower abundances of plants with palatable seeds in areas accessible to rodents, particularly in early succession. I found no significant difference in the abundances of plants with palatable seeds in early succession, however, where they averaged around 30% of cover in all treatments. This grassland was bordered by cropland on 3 sides and forest on the fourth. Perhaps birds, which had equal access to all plots, affected seed abundance more in this field than did rodents as Howe and Brown (1999) reported, even though my trapping data indicated substantial activity by rodents in the first years of succession.

As expected, greater abundances of plants with palatable seeds did occur in areas from which rodents had been excluded in mid-succession, a pattern that appeared primarily due to *Medicago sativa*. This legume decreased over time in all plots, but was present at significantly lower levels in plots to which rodents had access. This likely reflected the high palatability of its foliage to both vole species and its seeds to all three rodent species. In May 2005, however, a spike in abundance of palatable-seeded plants occurred in the plots to which rodents had access, likely because of *Thlaspi arvense*, which was relatively unpalatable to voles (Table 1). In 2004, vole populations in the mid-successional grassland reached the highest densities seen during this study and much of the vegetation in this field was devastated. The combination of the decreased cover (absolute, as well as relative) of

perennial grasses induced by the increased grazing by the vole population and the low palatability of *T. arvense* shoots allowed it to increase in abundance in spring 2005.

In late succession, I found greater abundance of plants with palatable seeds in areas accessible to mice and voles. *Medicago sativa* was not present in the late successional grassland and, thus, did not influence patterns of abundance there. Rather, the increase in abundance of *Poa pratensis*, a perennial grass with seeds highly palatable to *M. pennsylvanicus*, the dominant rodent in the community, largely accounted for the changes. Why then did the abundance of *P. pratensis* increase with vole access? This grass scored very low in palatability trials (Table 1), and the abundance of the more palatable dominant grass *Festuca arundinacea* decreased with vole access over this time period. This likely allowed more light and space for *P. pratensis*, which is low-growing and light-loving (Bugbee and Johnson 2005).

As expected, I found lower abundances of highly palatable forbs in areas accessible to the herbivorous voles in the mid-successional field, where substantial decreases in *M. sativa* occurred in areas with rodent access (discussed above). In early succession, mean abundances of palatable forbs (mostly *M. sativa*, which was planted) ranged between <1% and >40% cover because of highly variable water availability in this field (flooding and drought), so no treatment effects were detected. In late succession, there were very few highly palatable forbs overall (mean cover consistently <1% and often zero), but after 2 years of rodent exclusion, red clover (*T. pratense*), highly palatable to voles in this study and others (Zimmerman 1965, Lindroth and Batzli 1984, Marquis and Batzli 1989), appeared in two of the no-access plots in relative abundances as high as 4% cover. Similar increases in *Trifolium* occurred inside vole exclosures in Wyoming grassland (Sirotnak and Huntly 2000).



I had expected higher abundances of unpalatable species in areas with rodent access due to removal of palatable species by the herbivores, and did find an increase in unpalatable plants in mid- and late successional fields where rodents had access. In both fields, this pattern appeared driven by *Solidago canadensis*, a dominant, perennial, rhizomatous forb that increased steadily over time in plots with rodent access, but not in plots without rodent access. *Solidago canadensis* had just begun to colonize the early successional field by the last year of this study and, in spite of the lack of response to herbivory by palatable species in this field, *S. canadensis* occurred in significantly higher abundances in spring 2005 in m+v plots than in no-access plots (32.2% and 0% cover, respectively), while m-plots had intermediate abundances (16.3 % cover). Palatable forbs were extremely rare in late succession, so the increase in *S. canadensis* in that field was probably in response to decline in the dominant grass, *Festuca arundinacea*.

I had expected little, if any, response of perennial grasses to herbivory due to their basal meristems and their storage of nutrients in underground rhizomes. However, grasses highly palatable to voles in this study (*Bromus inermis*, *Dactylis glomerata*, *Festuca arundinacea*, and *Lolium perenne*) did respond with increased abundance inside rodent exclosures in both the mid- and late successional fields, suggesting a negative response to vole herbivory. In a California annual grassland, an increase in *Festuca*, a less preferred grass occurred at high vole (*M. californicus*) densities, when standing crop and seed crop of highly preferred species had been substantially reduced (Batzli and Pitelka 1970).

Although many studies have found negative effects of voles on woody seedlings (Ostfeld and Canham 1993; Ostfeld et al. 1997; Pusenius et al. 2000; Sullivan et al. 2001; Pusenius et al. 2003), I found no such effects in these grasslands. However, I only

occasionally encountered tree seedlings in the early and late successional grasslands, and never in the mid-successional grassland. More intense sampling or sites with greater recruitment of seedlings may be required to see an effect of voles.

Finally, I had expected the removal of herbivorous and granivorous activity to result in decreased species richness, evenness, or diversity of plants because foraging activities should extirpate or at least reduce abundances of highly palatable species, thereby increasing the dominance of unpalatable species. Once again, I found no effect of treatment in early succession. Contrary to my predictions, greater species evenness occurred in the plots to which mice and voles did have access in the late successional field. Species evenness in this grassland seemed strongly affected by the abundance of *Solidago canadensis*, that increased in abundance in old field grasslands over the course of succession, dying back each fall and sending up new sprouts in the spring. By the end of the growing season, *S. canadensis* shoots were >1 m tall and, though a field might appear strongly dominated by that one species, a variety of species grew underneath the goldenrod. This likely enabled areas with high abundances of *S. canadensis* to maintain higher evenness in spite of herbivory. In the plots without herbivore access, *Festuca arundinacea* (an introduced, perennial bunchgrass) increased in abundance, creating a much thicker cover with fewer plants surviving underneath.

In the mid successional grassland, as expected, higher evenness and diversity occurred in the plots without rodents. Very high vole densities occurred in this field in 2004 (Fig. 3.1) and, by late summer 2004, the understory below *S. canadensis* had virtually disappeared and voles which could occasionally be seen running across the ground. By growing rapidly in the spring and becoming fibrous and highly unpalatable to voles, *S.*

*canadensis* escapes herbivory, but apparently voles had consumed most other plants in this field. The refuge from herbivory inside the no-access exclosures resulted in greater evenness and diversity of plants there.

*Voles vs. mice.*- I designed the exclosures to separate the effects of the smaller, granivorous mice from the slightly larger, more herbivorous voles. Analysis of the data, however, indicated that I did not achieve this objective. I had designed the exclosures for the m-plots with 1.3 cm holes to allow access by mice and tested them with adult voles ( $\geq 40$  g) to be sure that voles could not move through holes of this size. Although I only trapped 3 juvenile voles inside the m-only plots, 25% of all voles trapped were in the size range of *Peromyscus* ( $\leq 30$  g) and, because young voles can be under-represented in live-trapping (Boonstra and Krebs 1978) and as populations increased during summer, juveniles and sub-adults may have done a large part of the foraging. For almost all of the significant differences in plant abundances attributable to the treatments applied in this study (Figs. 3.2 to 3.4), the m-plots and m+v plots had similar abundances and the no-access plots differed from those. In addition, measurements of zygomatic breadth (the widest portion of the skull) and body length indicate that there may be only a 1 mm difference in skull width with a 15 mm difference in body length between *P. leucopus* and the 2 vole species (*M. ochrogaster* and *M. pennsylvanicus*, Hoffmeister 1989, pp. 210, 232). Thus, in grasslands with increasing vole populations and diminishing amounts of high-quality food, the small holes in the sides of the exclosures probably did not effectively prevent foraging by substantial numbers of young voles.

*Conclusions.*- Although unable to separate the effects of mice and voles, their combined activities did substantially affect the plant communities of old fields. In theory, herbivores

should prefer annual plants, which typically have more chemical defenses (Davidson 1993), over perennials, thus hastening the progress of successional transition from dominance of annual plants to perennials. However, voles found most annual species unpalatable in my feeding trials and evidence from multiple studies shows that herbivory more frequently retards than accelerates succession (Davidson 1993).

The only other study to investigate effects of multiple small mammal species on plant communities in successional old fields (Bowers 1993) reported few effects due to little visitation by animals in years 1-4 of succession. While I documented regular visitation by mammals, even in the first year of succession, I still found few effects of rodents then. As succession progressed and perennial grasses and forbs increased in abundance, the animals' feeding preferences had greater influence on the relative abundance of plants in the communities.

Results of this study suggested greater effects of herbivory compared to those from granivory. Abundances of plants with palatable seeds were, as expected, less common in areas with rodent access in mid-succession, but this effect was attributable to one particularly palatable species (*Medicago sativa*) that was planted. This decline of the plant also accounted for the only decrease in palatable forbs attributable to rodents (in mid-succession). Goldenrod (*S. canadensis*), the unpalatable dominant forb in these old field grasslands, increased in abundance where voles had access, results similar to those found at high rodent densities in tallgrass prairie (Gibson et al. 1990). Palatable perennial grasses also responded to herbivory, achieving higher abundances without rodents in both the mid- and late successional fields.

Other studies of herbivory have found either positive or negative effects on diversity (Huntly 1991), and I found contrasting patterns in species evenness in mid- and late succession, likely attributable to differences in vole densities. Many exclosure studies have shown that feeding of herbivores upon less common species leads to increased dominance of the unpreferred species (Lindroth 1989, Gibson et al. 1990, Bowers 1993, Howe et al. 2002), whereas consumption of dominant species leads to increased plant species evenness and diversity (Weis 1975, Lindroth 1989, Howe and Brown 2000, Howe and Brown 2001, Olofsson et al. 2002). In my study, the mid-successional grassland had very high vole density, which led to low evenness and diversity when one unpalatable species came to dominate the community. The late successional grassland had with lower herbivore pressure and higher evenness among plant species.

Overall, effects of herbivory were greater than those of granivory, palatable plants decreased and unpalatable plants increased in abundance with rodent access and, not surprisingly, the influence of herbivory was most noticeable where the density of voles was highest. There was little overall effect of rodents on diversity of plant communities, but their influence on plant diversity differed between fields with varying herbivore pressure.

### Literature Cited

- BATZLI, G. O. 1977. Population dynamics of the white-footed mouse in floodplain and upland forests. *Am Midl Nat* 97: 18-32.
- BATZLI, G. O. and F. A. PITELKA. 1970. Influence of meadow mouse populations on California grasslands. *Ecology* 51(6): 1027-39.
- BOONSTRA, R. and C. KREBS. 1978. Pitfall trapping of *Microtus townsendii*. *J. Mamm.* 59: 136-148.

- BROWN, J. H. and E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- BUGBEE, B. and P. JOHNSON. 2005. Genetic characteristics and environmental parameters for growing turfgrass in closed and retractable dome stadiums. [http://www.usu.edu/cpl/research\\_turf.htm](http://www.usu.edu/cpl/research_turf.htm)
- COGSHALL, A. S. 1928. Food habits of deer mice of the genus *Peromyscus* in captivity. *J Mamm* 9: 217-21.
- COLE, F. R. and G. O. BATZLI. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. *Journal of Animal Ecology* 48: 455-470.
- CONNELL, J.H. and R.O. SLAYTER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- CONOVER, W. J.. 1980. Practical nonparametric statistics, 2nd edition. John Wiley and Sons, New York.
- DAVIDSON, D. W.. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23-35.
- DICKINSON, N. M. and A. POLWART. 1982. The Effect of Mowing Regime on an Amenity Grassland Ecosystem: Above-and Below-Ground Components. *Journal of Applied Ecology* 19: 569-577.
- ENGLISH, E. I. and M. A. BOWERS. 1994. Vegetation gradients and proximity to woodchuck (*Marmota monax*) burrows in an old-field. *Journal of Mammalogy* 75: 775-780.
- GETZ, L. L., J. E. HOFMANN, B. McGUIRE, and T. W. DOLAN III. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. *J. of Mammalogy* 82: 22-34.
- GIBSON, D. J., C. C. FREEMAN, and L. C. HURLBERT. 1990. Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia* 84: 169-175.
- GILL, D. S. and P. L. MARKS. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monographs* 61: 183-20
- HAKEN, A. E. and G. O. BATZLI. 1996. Effects of availability of food and interspecific competition on diets of prairie voles (*Microtus ochrogaster*). *J. Mamm.* 77: 315-324.

- HAMBACK, P. A., L. OKSANEN, P. EKERHOLM, A. LINDGREN, T. OKSANEN, and M. SCHNEIDER. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos* 106: 85-92.
- HOFFMEISTER, D. F.. 1989. *Mammals of Illinois*. University of Illinois Press.
- HOWE, H. F. and J. S. BROWN. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776-1781.
- HOWE, H. F. and J. S. BROWN. 2000. Early effects of rodent granivory on experimental forb communities. *Ecological Applications* 10: 917-924.
- HOWE, H. F. and J. S. BROWN. 2002. The ghost of granivory past. *Ecology Letters* 4: 371-378.
- HOWE, H. F., J. S. BROWN and A. B. ZORN. 2002. A rodent plague on prairie diversity. *Ecology Letters* 5: 30-36.
- HUNTLY, N.. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22: 477-503.
- KANTAK, G.E. 1983. Behavioral, seed preference and habitat selection experiments with two sympatric *Peromyscus* species. *Am Midl Nat* 109: 246-52.
- LANDE, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.
- LIN, Y. K. and G. O. BATZLI. 2001. The influence of habitat quality on dispersal, demography, and population dynamics of voles. *Ecological Monographs* 71: 245-75.
- LINDROTH, R. L. and G. O. BATZLI. 1984. Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. *J Mamm* 65: 600-606.
- LINDROTH, R. L. 1989. Mammalian herbivore-plant interactions. *in* *Plant-Animal Interactions*, ed. W. G. Abrahamson, McGraw-Hill.
- MARQUIS, R. J. and G. O. BATZLI. 1989. Influence of chemical factors on palatability of forage to voles. *J of Mammalogy* 70: 503-11.
- MITTELBAACH, G.G. and K.L. GROSS. 1984. Experimental studies of seed predation in old-fields. *Oecologia* 65: 7-13.
- MOHLENBROCK, R. H. 2002. *Vascular Flora of Illinois*. Southern Illinois University Press.

- OLFF, H. and M. E. RITCHIE. 1998. Effects of herbivores on grassland plant diversity. *TREE* 13: 261-265.
- OLOFSSON, J., J. MOEN, and L. OKSANEN. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos* 96: 265-272.
- OSTFELD, R. S. and C. D. CANHAM. 1993. Effects of meadow vole population density of tree seedling survival in old fields. *Ecology* 74: 1792-1801.
- OSTFELD, R. S., R. H. MANSON, and C. D. CANHAM. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1531-1542.
- PARMENTER, R. R., M. R. MENSCH, and J. A. MACMAHON. 1987. Shrub litter production in a sagebrush-steppe ecosystem: rodent population cycles as a regulating factor. *J. of Range Management* 40: 50-54.
- PASCARELLA, J. B. and M. GAINES. 1991. Feeding preferences of the prairie vole *Microtus ochrogaster* for seeds and plants from an old-field successional community. *Transactions of the Kansas Academy of Science* 94: 3-11.
- PUSENIUS, J., R. S. OSTFELD, and F. KEESING. 2000. Patch selection and tree-seedling predation by resident vs. immigrant meadow voles. *Ecology* 81: 2951-2956.
- PUSENIUS, J., K. PRITTINEN, H. ROININEN, and M. ROUSI. 2003. Effects of the availability of herbaceous food on vole attacks on birch seedlings. *Ecoscience* 10: 155-160.
- SAKAI, T. and H. HIROTA. 1990. Studies on the root mass accumulation with a secular change in six cool-season grass species. *Grassland Science* 36: 247-253.
- SAMSON, D. A., T. E. PHILIPPI, D. W. DAVIDSON. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos* 65:61-80.
- SARTZ, R. S.. 1970. Mouse damage to young plantations in southwestern Wisconsin. *J. of Forestry* 68: 88-89.
- SCHMIDT, B. and F. A. BAZZAZ. 1992. Growth responses of rhizomatous plants to fertilizer application and interference. *Oikos* 65: 13-24.
- SIROTNAK, J. M. and N. J. HUNTLY. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81: 78-87.



- SULLIVAN, T. P., D. S. SULLIVAN, and E. J. HOGUE. 2001. Influence of diversionary foods on vole (*Microtus montanus* and *Microtus longicaudus*) populations and feeding damage to coniferous tree seedlings. *Crop Protection* 20: 103-112.
- SWIHART, R.K. and R.H. YAHNER. 1982. Habitat features influencing use of farmstead shelterbelts by the eastern cottontail (*Sylvilagus floridanus*). *Am. Midl. Nat.* 107: 411-14.
- THOMPSON, D. Q.. 1965. Food preferences of the meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. *American Midland Naturalist* 74: 76-86.
- TILMAN, D.. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125: 827-52.
- WEIS, I. M. 1975. Alterations in a grassland plant community: the effects of microtine herbivory. Ph. D. dissertation, University of Iowa.
- WHITAKER, J. O. Jr. and R. E. MUMFORD. 1972. Ecological studies on *Reithrodontomys megalotis* in Indiana. *J. Mamm.* 53: 850-60.
- ZAR, J. H.. 1996. Biostatistical analysis. Prentice-Hall.
- ZIMMERMAN, E. G. 1965. A comparison of habitat and food of two species of *Microtus*. *J. Mamm.* 46: 605-12.

Table 3-1. Weighted mean herbivory scores for plant palatabilities (spring, summer, and fall) by the three most common mammal species. *Microtus pennsylvanicus* was not present in the early successional grassland and, therefore, not fed plants only found in that field. Status in Illinois (N= native, I= introduced), life history (A= annual or biennial, P= perennial), growth forms (F= forb, G= graminoid, W= woody), and mean palatability scores for plant species. Woody plants tested at immature, herbaceous stage indicated by (imm). Plants not available in spring indicated by <sup>1</sup>, those not available in fall indicated by <sup>2</sup>.

Plant species	Origin	Life history	Growth form	<i>M. ochrogaster</i>		<i>M. pennsylvanicus</i>		<i>P. leucopus</i>	
				N	mean	N	mean	N	mean
<i>Trifolium pratense</i>	I	A	F	15	2.7	19	2.8	15	0.4
<i>Medicago sativa</i>	I	P	F	16	2.5	21	3.0	22	0.6
<i>Taraxacum officinale</i>	I	P	F	15	2.5	22	2.4	15	0.5
<i>Lolium perenne</i>	I	P	G	15	2.3	15	1.0	15	0.3
<i>Dactylis glomerata</i>	I	P	G	15	2.0	15	1.7	15	0.0
<i>Festuca arundinacea</i>	I	P	G	15	1.9	15	2.4	15	0.3
<i>Ambrosia trifida</i> <sup>1</sup>	N	A	F	12	1.8	15	0.7	10	0.5
<i>Bromus japonicus</i> <sup>2</sup>	I	A	G	15	1.4	10	1.2	15	0.0
<i>Rumex crispus</i>	I	P	F	15	1.1	20	1.0	15	0.0
<i>Phleum pratense</i>	I	P	G	15	1.1	15	1.1	15	0.7
<i>Thlaspi arvense</i> <sup>2</sup>	I	A	F	9	1.0	11	0.4	11	1.0
<i>Carex laevivaginata</i>	N	P	G	15	0.9	15	1.9	15	1.0
<i>Polygonum persicaria</i>	I	A	F	15	0.8	--	--	20	0.9
<i>Rosa multiflora</i> (imm)	I	P	F	15	0.8	17	0.8	15	0.0
<i>Chamaesyce maculata</i> <sup>1</sup>	N	A	F	8	0.8	--	--	10	0.0
<i>Aster ericoides</i>	N	P	F	15	0.8	15	1.2	17	0.1
<i>Abutilon theophrasti</i> <sup>1</sup>	I	A	F	11	0.8	--	--	14	1.9
<i>Setaria viridis</i> <sup>1</sup>	I	A	G	15	0.8	--	--	21	0.7
<i>Conyza canadensis</i> <sup>1</sup>	N	A	F	10	0.8	--	--	17	0.0
<i>Sida spinosa</i> <sup>1</sup>	I	P	F	9	0.7	--	--	12	0.8
<i>Pastinaca sativa</i>	I	A	F	18	0.7	17	0.2	15	1.0
<i>Calystegia sepium</i> <sup>1</sup>	N	P	F	10	0.7	10	0.0	10	0.0
<i>Solidago canadensis</i>	N	P	F	15	0.6	17	0.8	15	0.0
<i>Vitis palmate</i> (imm)	N	P	F	15	0.6	15	0.5	15	0.8
<i>Amaranthus retroflexus</i> <sup>1</sup>	I	A	F	12	0.6	--	--	18	0.2
<i>Viola affinis</i>	N	A	F	15	0.5	15	0.7	15	0.0
<i>Oxalis corniculata</i>	I	P	F	15	0.5	--	--	15	0.0
<i>Elymus canadensis</i>	N	P	G	15	0.5	15	1.4	15	0.0
<i>Panicum capillare</i> <sup>1</sup>	N	A	G	4	0.5	--	--	--	--
<i>Physalis subglabrata</i> <sup>1</sup>	N	P	F	10	0.4	--	--	10	0.0
<i>Bromus inermis</i>	I	P	G	15	0.4	15	2.9	15	0.0
<i>Geum canadense</i>	N	P	F	15	0.4	15	0.4	15	0.0
<i>Poa pratensis</i>	I	P	G	15	0.4	17	0.2	16	0.0
<i>Asclepias syriaca</i>	N	P	F	12	0.4	13	0.2	12	0.5
<i>Cirsium arvense</i>	I	P	F	10	0.4	17	0.0	15	0.0
<i>Barbarea vulgaris</i>	I	A	F	17	0.3	23	0.2	10	1.3
<i>Solanum ptychanthum</i> <sup>1</sup>	N	P	F	9	0.3	--	--	10	0.8
<i>Echinochloa crus-galli</i> <sup>1</sup>	I	A	G	13	0.2	--	--	12	1.3
<i>Cerastium fontanum</i>	I	P	F	10	0.0	15	1.5	10	0.0
<i>Vernonia gigantea</i>	N	P	F	12	0.0	15	0.6	10	0.0
<i>Solanum carolinense</i>	N	P	F	10	0.0	17	0.5	12	0.5
<i>Digitaria sanguinalis</i> <sup>1</sup>	I	A	G	10	0.0	--	--	10	0.0

Table 3-2. Mean weight of seeds  $\pm SE$  consumed by the three species of mammal most common in successional grasslands (number of trials in parentheses). Seed sizes are categorized as large (L,  $>1.5\text{mg}$ ) or small (S,  $<1.5\text{ mg}$ ).

Plant species	Seed weight (mg)	Seed size	Mean consumption (g/24 hrs)		
			<i>P. leucopus</i>	<i>M. ochrogaster</i>	<i>M. pennsylvanicus</i>
<i>Ambrosia trifida</i>	39.3	L	$1.260 \pm 0.469$ (5)	$0.114 \pm 0.066$ (5)	$0.105 \pm 0.105$ (5)
<i>Setaria viridis</i>	0.7	S	$0.840 \pm 0.238$ (7)	$0.705 \pm 0.468$ (5)	--
<i>Phleum pratense</i>	0.5	S	$0.763 \pm 0.274$ (7)	$0.133 \pm 0.098$ (5)	$0.601 \pm 0.117$ (5)
<i>Elymus canadensis</i>	3.3	L	$0.716 \pm 0.142$ (5)	$0.721 \pm 0.299$ (5)	$0.607 \pm 0.235$ (5)
<i>Pastinaca sativa</i>	1.0	S	$0.655 \pm 0.147$ (6)	$0.080 \pm 0.080$ (5)	$0.850 \pm 0.234$ (5)
<i>Sida spinosa</i>	2.6	L	$0.617 \pm 0.294$ (5)	$0.700 \pm 0.355$ (4)	--
<i>Abutilon theophrasti</i>	9.8	L	$0.604 \pm 0.121$ (9)	$0.136 \pm 0.092$ (5)	--
<i>Medicago sativa</i>	1.7	L	$0.385 \pm 0.082$ (6)	$0.212 \pm 0.105$ (5)	$0.130 \pm 0.101$ (5)
<i>Thlaspi arvense</i>	0.1	S	$0.356 \pm 0.124$ (5)	$0.046 \pm 0.019$ (5)	$0.063 \pm 0.018$ (5)
<i>Bromus japonicus</i>	2.3	L	$0.312 \pm 0.172$ (5)	$0.116 \pm 0.050$ (5)	$0.060 \pm 0.012$ (5)
<i>Trifolium pratense</i>	1.3	S	$0.250 \pm 0.057$ (7)	$0.360 \pm 0.132$ (5)	$0.118 \pm 0.050$ (5)
<i>Polygonum persicaria</i>	1.4	S	$0.198 \pm 0.068$ (8)	$0.056 \pm 0.027$ (5)	--
<i>Asclepias syriaca</i>	4.6	L	$0.143 \pm 0.114$ (5)	$0.020 \pm 0.013$ (5)	$0.005 \pm 0.004$ (5)
<i>Lolium perenne</i>	3.3	L	$0.124 \pm 0.042$ (5)	$0.010 \pm 0.006$ (5)	$0.000 \pm 0.000$ (5)
<i>Carex cephalophora</i>	2.6	L	$0.098 \pm 0.071$ (6)	$0.123 \pm 0.043$ (5)	$0.590 \pm 0.157$ (5)
<i>Barbarea vulgaris</i>	2.3	L	$0.086 \pm 0.054$ (5)	$0.120 \pm 0.050$ (5)	$0.032 \pm 0.014$ (5)
<i>Bromus inermis</i>	0.9	S	$0.051 \pm 0.012$ (7)	$0.048 \pm 0.027$ (5)	$0.064 \pm 0.020$ (5)
<i>Rumex crispus</i>	0.7	S	$0.048 \pm 0.024$ (7)	$0.027 \pm 0.017$ (5)	$0.041 \pm 0.019$ (5)
<i>Echinochloa crus-galli</i>	0.8	S	$0.045 \pm 0.041$ (5)	$0.312 \pm 0.212$ (5)	--
<i>Festuca arundinacea</i>	1.2	S	$0.044 \pm 0.019$ (7)	$0.007 \pm 0.007$ (5)	$0.030 \pm 0.021$ (5)
<i>Poa pratensis</i>	0.3	S	$0.040 \pm 0.013$ (5)	$0.054 \pm 0.029$ (5)	$0.451 \pm 0.190$ (5)
<i>Digitaria sanguinalis</i>	0.7	S	$0.017 \pm 0.017$ (4)	--	--
<i>Dactylis glomerata</i>	0.4	S	$0.008 \pm 0.004$ (5)	$0.044 \pm 0.021$ (5)	$0.110 \pm 0.087$ (5)

Figure 3.1. Numbers of different individuals of small mammal species trapped in A) an early successional, B) a mid-successional, and C) a late successional old field.

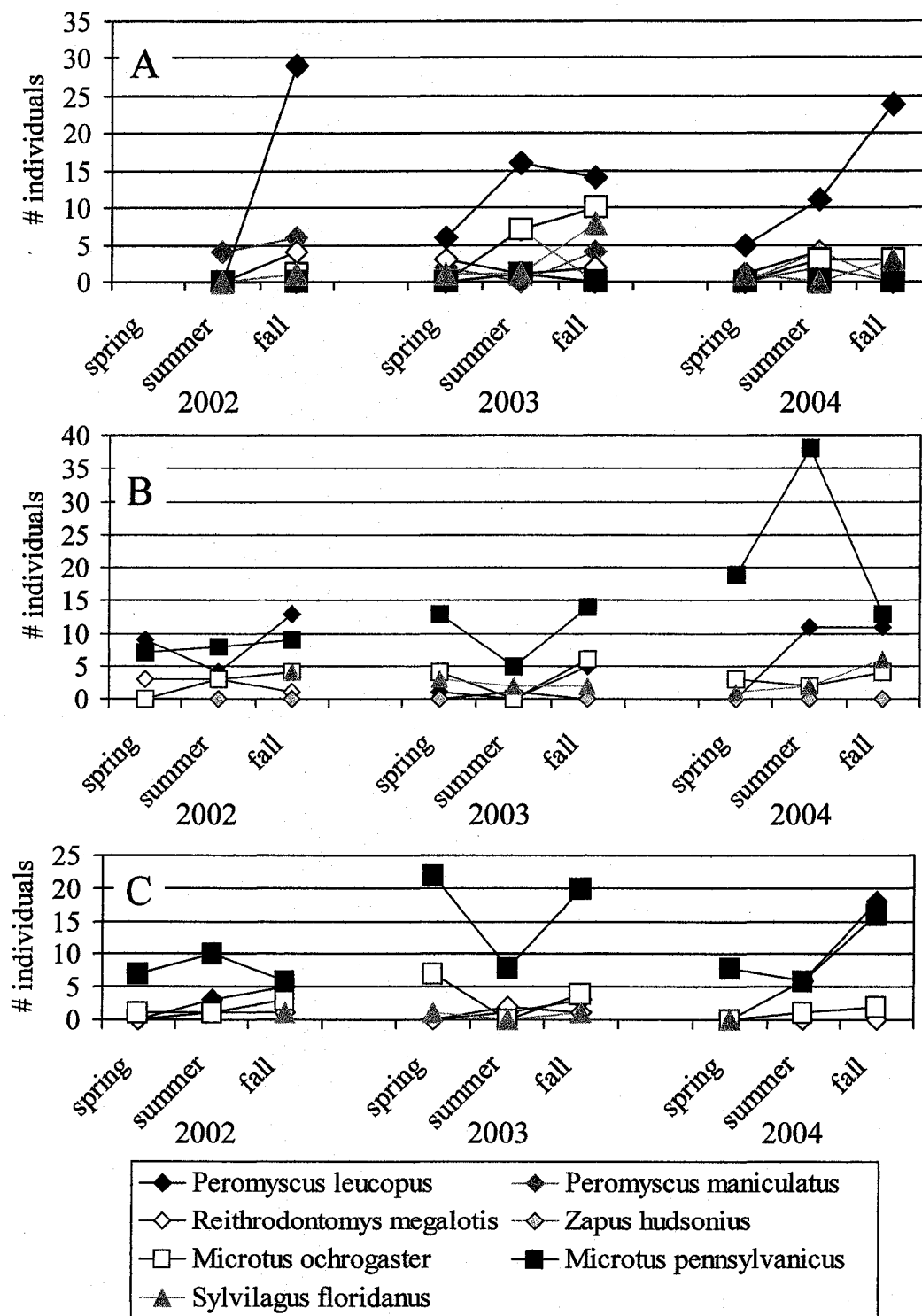


Figure 3.2. Mean ( $\pm 1 SE$ ) relative abundances of plants with palatable seeds under three treatments in A) a mid-successional and B) a late successional old field in September (S), May (M), and July (J) 2001 to 2005. Treatments with access by no small mammals, by mice only, or by mice and voles, all with 3 replicates.

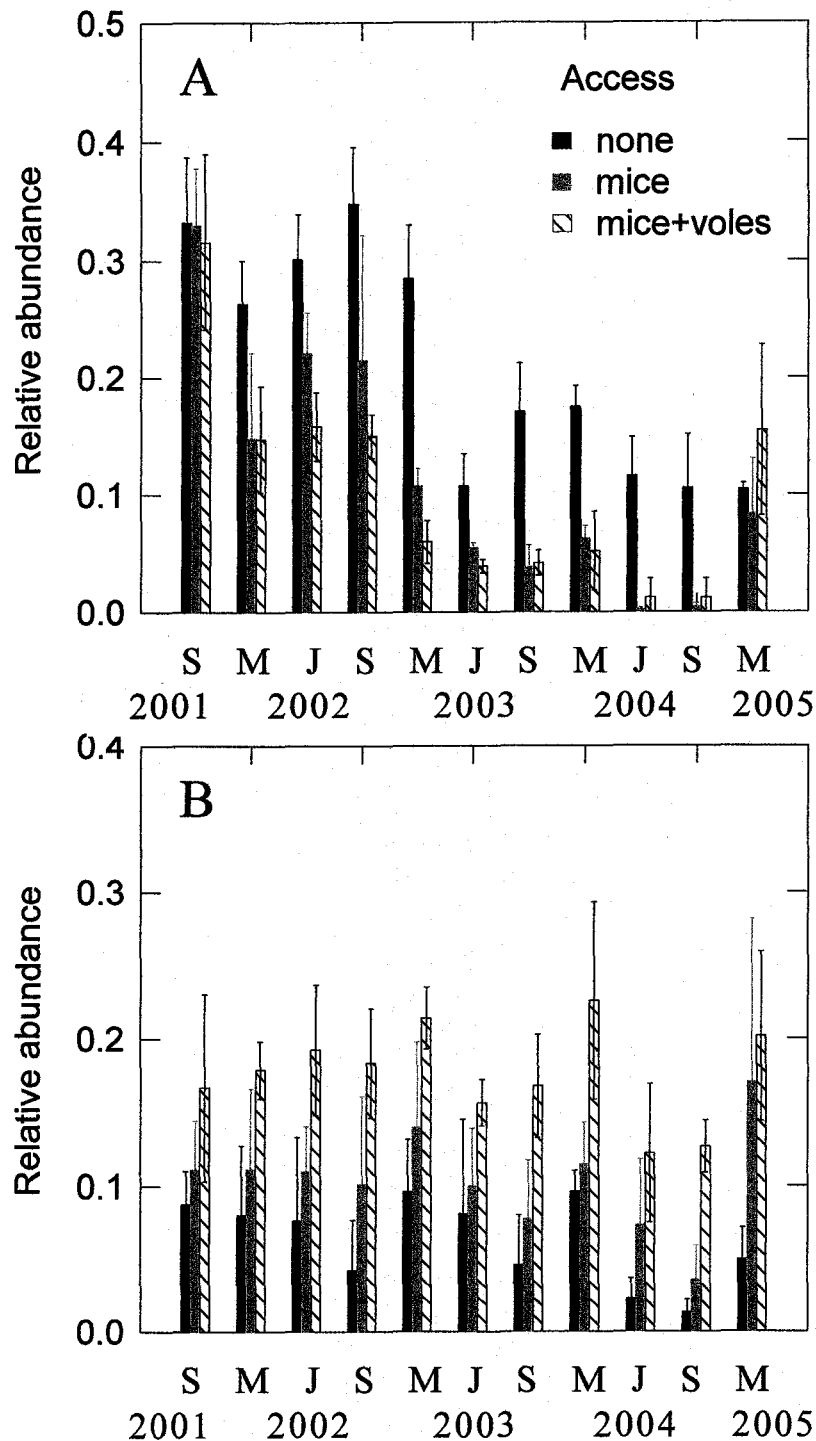


Figure 3.3. Mean ( $\pm 1$  SE) relative abundances of A) palatable forbs in mid-succession, B) palatable graminoids in mid-succession, and C) palatable graminoids in late succession in September (S), May (M), and July (J) 2001 to 2005. Treatments with access by no small mammals, by mice only, or by mice and voles, all with 3 replicates.

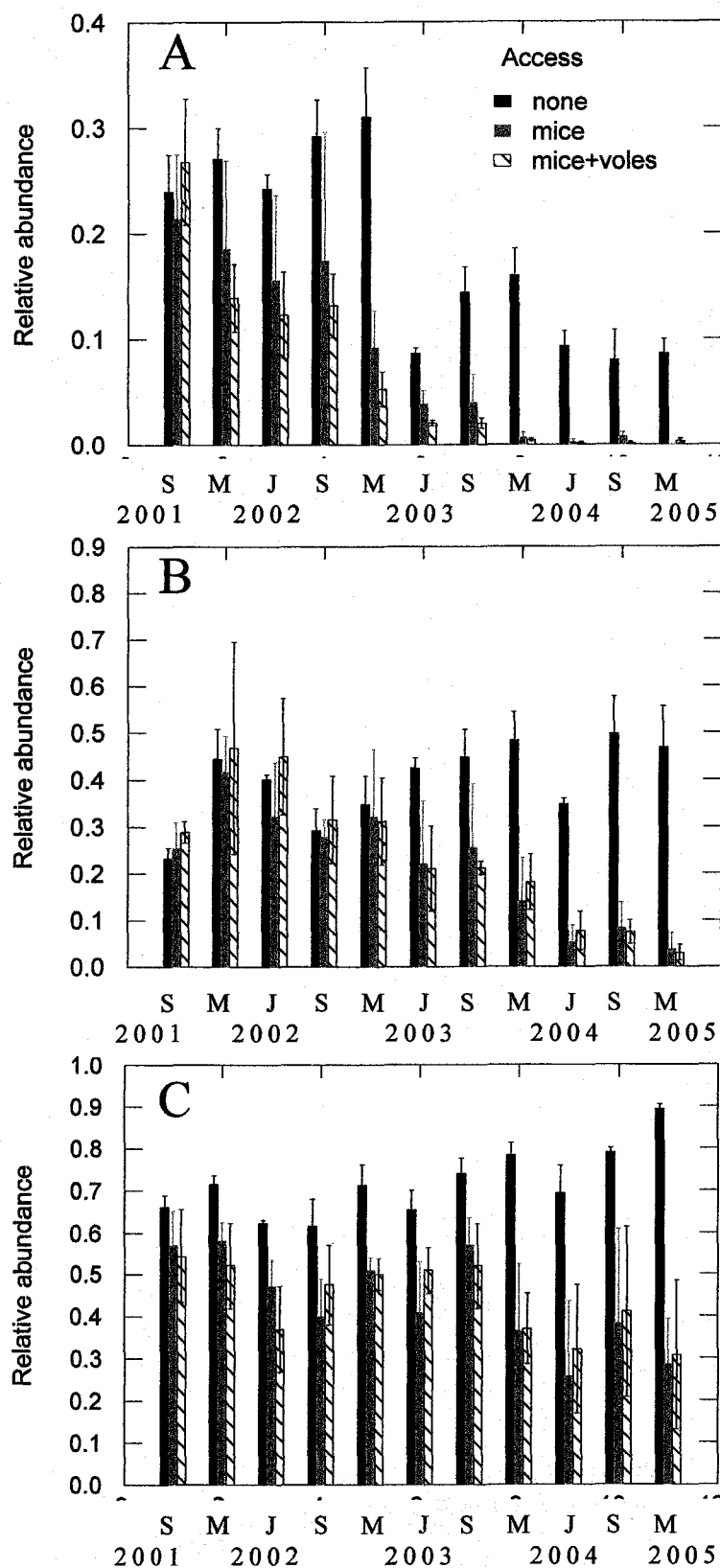


Figure 3.4. Mean ( $\pm 1 SE$ ) relative abundances of unpalatable plants in A) a mid successional and B) a late successional old field in September (S), May (M), and July (J) 2001 to 2005. Treatments with access by no small mammals, by mice only, or by mice and voles, all with 3 replicates.

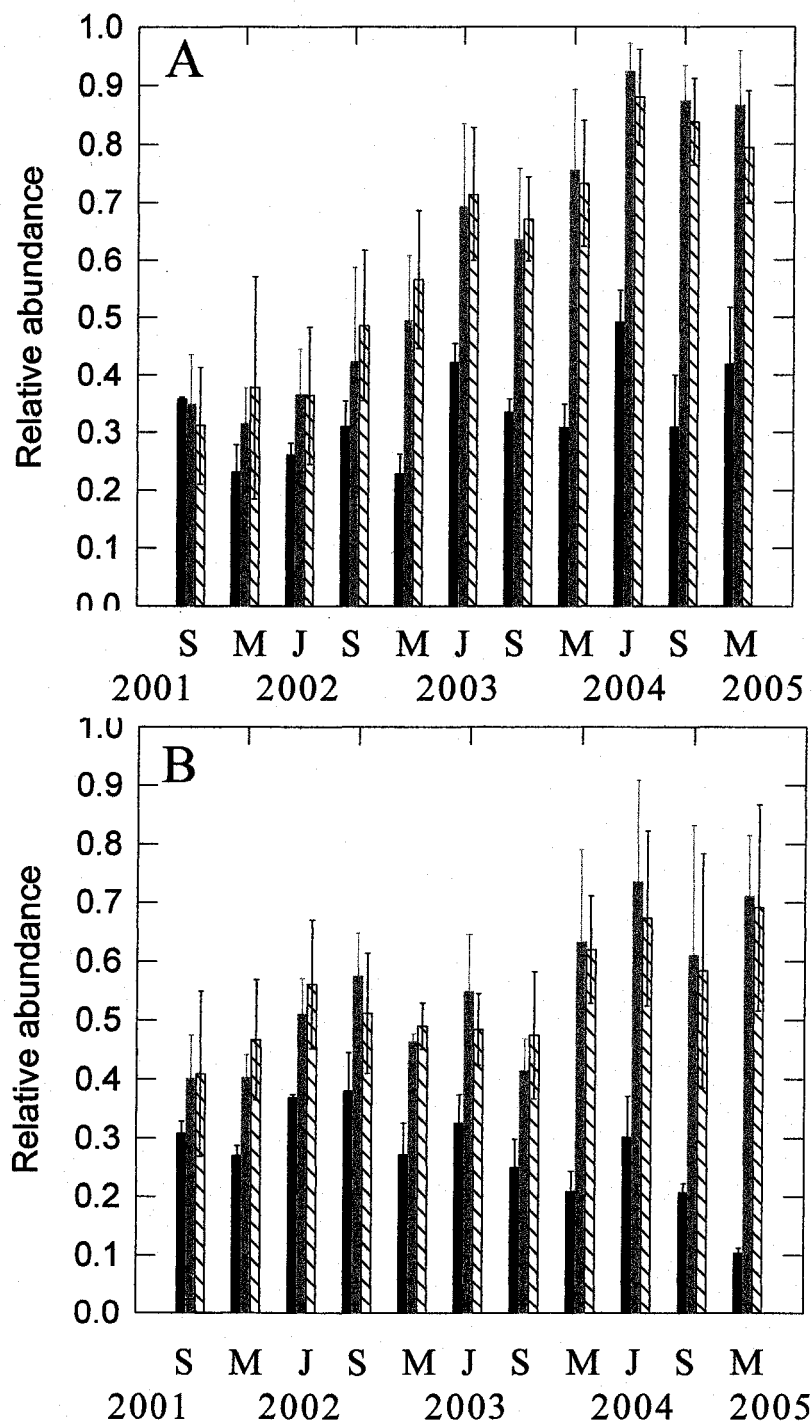
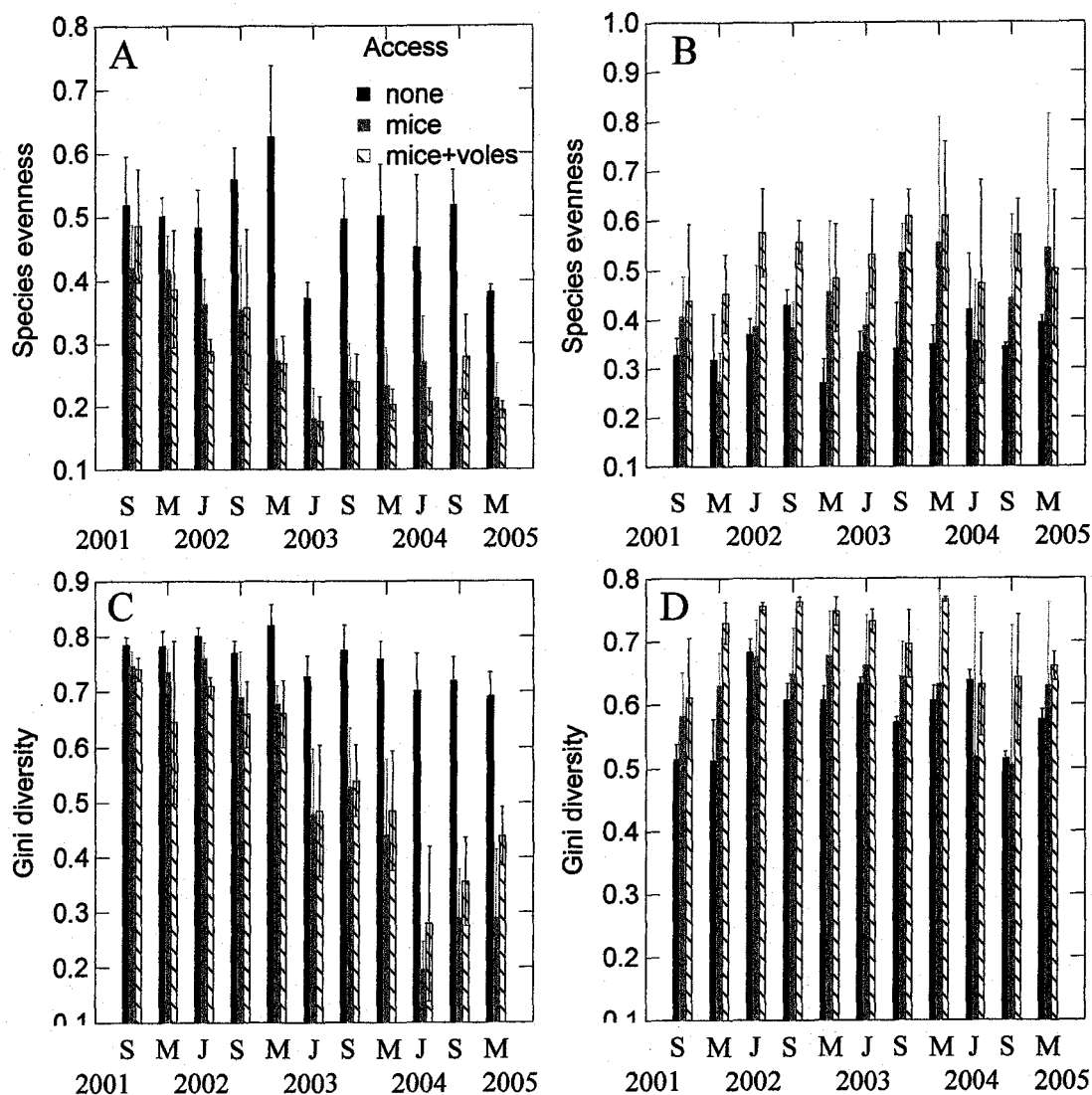


Figure 3.5. Mean ( $\pm 1$  SE) for A) species evenness in mid-succession, B) species evenness in late succession, C) Gini coefficient of diversity in mid-succession, and, D) Gini coefficient of diversity in late succession in September (S), May (M), and July (J) 2001 to 2005. Treatments with access by no small mammals, by mice only, or by mice and voles, all with 3 replicates.





## CHAPTER 4

### EFFECTS OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) ON SUCCESSIONAL GRASSLANDS

#### Introduction

Densities of white-tailed deer (*Odocoileus virginianus*) have reached record highs in recent decades in the midwestern U.S. (Nixon et al. 2001). Numerous studies have shown that browsing by deer can alter the composition of tree seedlings and saplings in forests, slowly leading to a community of less palatable tree species (Anderson and Katz 1993, Augustine and Jordan 1998, Gill and Beardall 2001, Russell et al. 2001, Rooney and Waller 2003). Deer also forage selectively on the herbaceous understory in forests and can even eliminate preferred plants, such as lilies and orchids (Nixon et al. 1991, Waller and Alverson 1997, Russell et al. 2001, Rooney and Waller 2003). Some studies in grasslands have shown that deer browsing reduces growth rates of woody seedlings and saplings and slows the rate of succession (Inouye et al. 1994, Knapp et al. 2002). In remnants of tallgrass prairies, Anderson et al (2001, 2005) found that deer negatively impacted standing biomass and reproductive capacities of preferred forbs so that unpalatable forbs and grasses increased in abundance.

While agriculture and development have destroyed 99.9% of the native prairies in Illinois (IDENR 1994), recent surveys report that over 19% of current land cover in Illinois is grassland (CTAP 2001). Most of these grasslands, formed on abandoned croplands (oldfields), roadsides, and bufferstrips, are dominated by introduced, perennial grasses such as *Festuca arundinacea*, *Poa pratensis*, and *Bromus inermis* (CTAP 2001). The resulting fragmented landscape of wooded patches, agricultural fields, and non-native grasslands

forms ideal habitat for deer (Cornicelli et al. 1996), but I found no studies of the impact of deer in these grasslands. To identify the changes in the plant communities caused by deer herbivory, I designed an experiment to exclude deer from plots in oldfields at different successional stages

Because deer forage selectively on forbs in the growing season and on woody plants in the winter, I hypothesized that activity of deer would 1) decrease the proportion of forbs in the plant community and increase the proportion of graminoids, 2) decrease the proportion of woody seedlings and saplings in the plant community, and 3) decrease the diversity of the plant community. Although other activities of deer, such as trampling and seed dispersal, could also affect plant communities, I do not test hypotheses related to those mechanisms here.

## Methods

*Study sites.* - Because I wanted to examine the effects of deer over the course of succession from agricultural fields to mature grassland, I conducted my experiments in 3 old fields in different stages of succession. Although I chose the fields to represent different stages of succession, I recognize that some differences might reflect local conditions rather than successional stage. To minimize site differences, I chose old fields that occurred within 1 km of one another at the Ecological Research Area of the University of Illinois located 5 km northeast of Urbana, Illinois. All fields had similar soils (silt loam or silty clay loam) and drainage (flat topography), and each was planted to alfalfa in spring after disking the remnants of the proceeding fall's crop. The early successional field was released from agriculture in the fall of 2001, the mid-successional field in fall of 1998, and the late

successional field in fall of 1989. Natural colonization of the fields followed without further disturbance, except for dormant mowing of the late successional field for several years before the start of this experiment.

*Exclosure experiments.* - In each successional field, as part of a larger study of mammalian herbivory, I constructed 4-m by 4-m exclosures that allowed access of various combinations of mammalian herbivores to the vegetation depending upon the size of mammal. In fall 2001 and spring 2002, I established exclosures for different groups of small mammals and control plots (5 treatment levels with 3 replicates each) at random locations within a 50 X 100 m grid that had 4 m between plots in each row and 8 m between plots in each column. In spring and early summer 2003, I added three deer exclosures to the 50 X 100 grid. The deer exclosures were constructed with 2-m tall wire fencing (5 cm X 15 cm mesh) attached to corner posts 4 m apart and raised 30 cm above ground level to allow access by all other herbivores. Although enterprising deer might jump over such fences, getting out of the small space would likely cause substantial destruction, and I saw no sign that deer ever entered the exclosures (no damage, no feces, no signs of foraging). The control plots had only corner stakes.

Because of the need for repeated sampling of vegetation, I used a non-destructive method to compare the differences in vegetation among treatments. Vegetation grew too high for convenient point sampling, so I estimated the contribution to cover of all species of vascular plants found in 6 permanent 0.5 X 1.5-m quadrats (4.5 m total area) located within each treatment plot. I placed a 0.5 X 1.5-m plastic frame, divided into 12 equal sections with taut string, over each quadrat to organize my observations. To obtain accurate estimates of percent cover, I recorded the number of small sections (12.5 X 12.5-cm) covered by each

plant species within each quadrat (48 sections per quadrat for a total of 288 per sample) during each sampling period. To encompass changes in vegetation throughout the growing season, I sampled each spring (May), summer (July), and autumn (September) from the time the plots were established through September 2005. Because absolute cover estimates varied among seasons and years and could exceed 100%, I transformed the values for each species into relative cover (% of total within each sampling plot) to analyze composition of the vegetation. Species identification and nomenclature followed Mohlenbrock (2002).

*Statistical methods.*— To determine similarity of the control and treatment plots at the beginning of the experiment, I summarized vegetation data for the first season in which the deer exclosures were established (spring 2003 for mid and late succession, summer '03 for early succession). I compared the community composition for the control and treatment plots based upon the relative abundance of plant species using the Mann-Whitney U-test (MW), the non-parametric equivalent of the t-test (Zar 1996, p. 198), because I could not transform the cover data to reflect a normal distribution. I also categorized the data into groups that would be used to test my hypotheses (forbs, grasses, woody plants) and calculated measures of community diversity. I conducted t-tests on these data (which were normally distributed) to determine if *a priori* differences existed between the control and exclosure plots.

To test my hypotheses, I categorized the data on relative abundances of plant species and in the control and treatment plots as forbs, graminoids, or woody seedlings/saplings for each sampling period (spring 2003 to summer 2005) and conducted repeated-measures ANOVA with the deer access as the between-plots factor and sampling period as within-plots factors. When I was unable to establish normal distributions for the response variables, I conducted analyses with rank-transformed data (Conover 1980).

To help interpret patterns found when hypothesis testing, I examined effects of deer on individual species by comparing the abundance of each plant species with a t-test on the control and exclosure treatments for the sampling period in question. If the data for a species were not normally distributed, I used the Mann-Whitney U-test (MW).

I could not use multivariate analyses of community structure nor repeated measures MANOVA because I had relatively few samples for each treatment each season in each field ( $n = 3$ ). Given this small sample size, I set the significance level for all analyses at  $P=0.100$  to reduce type II error. Although multiple comparisons of treatments on different plant species may lead to underestimates of type I error, these tests were only done to help interpret results found by hypothesis testing and not as post-hoc analyses, so I did not adjust significance levels using Bonferroni corrections.

Finally, I considered plant community structure by analyzing species richness, evenness, and diversity in all sampling plots. I calculated evenness based on Simpson's index of evenness (Krebs 1999, p. 449):  $E = (1/\sum p_i^2)/S$  where  $p_i$  is the proportion of cover for the  $i^{\text{th}}$  species and  $S$  is the number of species in the sample. A value near 0 indicates low evenness while a value closer to 1 indicates that the same proportion in each species. I used Gini's coefficient of diversity for the most unbiased index of diversity because of low values for evenness and small sample sizes (Lande 1996):  $G = 1 - \sum p_i^2$ . I omitted the correction factor for number of individuals in the sample ( $N/N-1$ ) because my samples were always based upon cover estimated using 288 small quadrats. Linear probability plots indicated that these data were normally distributed, so I conducted repeated-measures ANOVA for community structure on untransformed data.

## Results

### TESTING OF HYPOTHESES

*Early succession.* – In the first season in the early successional grassland (summer 2003), there were significantly greater abundances of forbs in areas outside the exclosures than areas inside (means of 96.1% and 93.1% cover, respectively;  $t\text{-stat}=3.242$ ,  $P=0.032$ ). However, by summer 2004, there were greater abundances of forbs in areas from which the deer had been excluded (means of 49.1% cover with and 63.2% cover without deer). This pattern of more forbs without deer access continued throughout 2005, although the difference was not statistically significant (RM-ANOVA,  $F_{1,4}=2.356$ ,  $P=0.200$ ; Fig. 4.1a). There were no significant interactions with treatment (RM-ANOVA,  $P>0.6$  for all cases).

With the exception of the occasional woody seedling, grasses formed the remainder of plant cover; the abundances of grasses showed the opposite pattern of the forbs, with initially significantly lower abundances of grasses with deer than without (means of 2.6% and 6.4% cover, respectively;  $t_{3,3}=-3.487$ ,  $P=0.025$ ), but changing to more grasses in areas with deer and fewer without deer by summer 2004, although again not statistically significant (average cover 50.0% and 36.1% respectively; RM-ANOVA,  $F_{1,4}=2.515$ ,  $P=0.188$ ). There were no significant interactions with treatment (RM-ANOVA,  $P>0.600$  for all).

Examining the abundances of the individual plant species in the first season, I found significant differences in the abundance of only one species, the annual grass *Setaria viridis*, which was more common inside the deer exclosures (mean cover without deer 6.1%, with deer 2.6%; Fig. 4.2a). The response of this species to the deer exclosures over time seemed to be driving the differences between the treatment levels for grasses. The abundances of *S. viridis* in the control and exclosure plots in summer 2004 were not different ( $t_{3,3}=0.568$ ,

$P=0.600$ ), but by summer 2005 this species was significantly more abundant in the control plots than inside the exclosures (mean cover without deer 37.4%, with deer 11.4%;  $t_{3,3}=2.157$ ,  $P=0.097$ ).

There were no differences in abundances of woody seedlings between deer exclosures and control plots at the start of the study ( $t_{3,3}=0.788$ ,  $P=0.475$ ) nor for the remainder of the study (RM-ANOVA,  $F_{1,4}=1.202$ ,  $P=0.334$ ; Fig. 4.1b). However, abundances of *Prunus serotina* and *Gleditsia triacanthos* were significantly higher inside exclosures than in control plots and, in fact, were only observed inside the plots to which deer had access ( $U_{3,3}=262.5$ ,  $P=0.038$  and  $U_{3,3}=273$ ,  $P=0.019$ , respectively; Fig. 4.3a-b).

*Mid-succession.* – In the first season of deer exclosures in the mid-successional grassland (spring 2003), there were no significant differences in the relative abundances of forbs or grasses ( $t_{3,3}=-0.883$ ,  $P=0.427$  and  $t_{3,3}=1.036$ ,  $P=0.359$ , respectively). No woody seedlings or saplings occurred in any of the experimental plots throughout the experiment. Examining the abundances of the individual plant species, I found only a significant difference in the abundances of *Taraxacum officinale* ( $t_{3,3}=-2.270$ ,  $P=0.086$ ) and a marginally significant difference in *Ambrosia trifida* ( $U_{3,3}=1.5$ ,  $P=0.121$ ); both were in greater abundances inside the deer exclosures (mean cover 4.3% and 0.3%, respectively) than in the control plots (mean cover 2.5% and 0.0%, respectively). After that first sampling period, however, *T. officinale* occurred consistently in higher abundances in plots with deer access, with a statistically significant difference in spring 2005 ( $t_{3,3}=2.828$ ,  $P=0.047$ ). *Ambrosia trifida*, on the other hand, had similar relative abundances on both control and deer exclosure plots throughout both 2004 and 2005, although I observed deer foraging on this plant.

Repeated-measures ANOVAs indicated a significant difference in the abundances of grasses and forbs in the mid successional grassland ( $F_{1,4}=8.106$ ,  $P=0.047$  for both) and a significant interaction between access and year ( $P<0.001$ ). Relative abundances of grasses decreased significantly over time inside deer exclosures while the abundance of forbs increased significantly over time inside the deer exclosures (Fig. 4.1b). Examination of patterns of abundance in individual plant species revealed significantly greater abundances *Festuca arundinacea* in areas with deer access than in deer exclosures (average cover with deer 32.6%, without deer 20.1%;  $U_{3,3}=283.5$ ,  $P=0.005$ ; Fig. 4.2b). *Cirsium arvense* had the opposite trend, with greater abundances inside deer exclosures than in control plots, although high variability kept the overall difference from statistical significance ( $U_{3,3}=212.5$ ,  $P=0.111$ ; Fig. 4.4b).

Five additional species of the 23 species tested had overall P-values  $< 0.100$  (see Appendix), but the differences in the abundances of these species were likely due to pre-existing vegetation patterns. Although initial analyses did not indicate statistically significant differences in any of these species at the beginning of the experiment, I had very low power to detect weak differences ( $N=3$ ) and trends for these plants did not change through time. *Solidago canadensis*, for example, had higher abundance inside deer exclosures than in control plots throughout the study (Fig. 4.5b). *Dactylis glomerata* had variable abundance in control plots throughout the study and always occurred at low abundance inside the exclosures. Abundances of *Ambrosia trifida*, *Bromus inermis*, and *Plantago major* also were highly variable, but all occurred more frequently inside the deer exclosures than in control plots.



*Late succession.* – In the first season in the late successional grassland (spring 2003), there were no significant differences in relative abundances of grasses, forbs, or woody seedlings ( $t_{3,3} < 0.71$ ,  $P < 0.34$  in all cases). Of the 17 plant species in our plots at this time, we found only one (*Carex cephalophora*) for which abundances were significantly different between the control and deer exclosure plots (mean cover with deer 0.5%, without deer 3.6%;  $t_{3,3} = -5.297$ ,  $P = 0.004$ ).

Repeated-measures ANOVAs showed no significant differences in abundances of grasses or forbs and no significant interactions ( $F < 0.51$ ,  $P > 0.51$  in all cases; Fig. 4.1c). Of the 31 plant species present in the plots, I found statistically significant differences in relative abundances of 12 (MW,  $P < 0.10$  in all cases; see Appendix). *Poa pratensis* and *Bromus inermis* were both more abundant in control plots than inside exclosures, a trend that was present at the beginning of the study and continued throughout the duration. *Rosa multiflora*, *Ambrosia trifida*, *Physalis subglabrata*, *Aster ericoides*, *Viola affinis*, *Calystegia sepium* were all more abundant inside deer exclosures than in control plots, although their occurrences within plots were highly variable. With the exception of *A. ericoides*, the mean abundances of these species never reached 1% cover, and abundance inside individual plots varied between 0% and 2.5% cover. Mean cover of *A. ericoides* reached almost 3% in the fall seasons, with abundance inside plots between 0 and 8.5% cover. *Cirsium arvense*, on the other hand, appeared strongly affected by deer ( $U_{3,3} = 200$ ,  $P = 0.014$ ; Fig. 4.4c). Its abundance was similar in the two treatments in 2003, but the difference between plots with and without deer access increased over time; in the summers of 2003, 2004, and 2005, cover averages in control plots were 2.0%, 1.6%, and 1.2% while inside the deer exclosures they were 2.7%, 5.4%, and 6.0%.

Overall abundance of woody seedlings was not significantly different between the control and deer exclosure plots ( $F_{1,4}=0.570$ ,  $P=0.492$ ), although this category did include 3 of the species for which I found statistically significant differences. *Prunus serotina* and *Gleditsia triacanthos* occurred more frequently encountered inside the deer exclosures than in the control plots but both were present there at the beginning of the experiment (Fig. 4.3c, 3d), while a third species (*Morus alba*) showed the opposite trend throughout the experiment ( $U_{3,3}>290$ ,  $P<0.08$  in all cases).

### COMMUNITY STRUCTURE

In the first season, there were no differences in any measures of community structure (richness, evenness, and diversity) between the control and deer exclosure plots in early succession ( $t_{3,3}<1.0$ ,  $P\geq 0.388$  in all cases), mid-succession ( $t_{3,3}<0.71$ ,  $P\geq 0.519$  in all cases), or late succession ( $t_{3,3}<1.6$ ,  $P>0.21$  for all cases). Similarly, I found no significant differences in any of the measures due to treatment or any significant interactions in early succession (RM-ANOVA,  $F_{1,4}<3.7$ ,  $P>0.12$ ), mid-succession ( $F_{1,4}<1.3$ ,  $P>0.31$ ), or late succession ( $F_{1,4}<0.64$ ,  $P>0.471$ ), although there was a trend for greater species richness in areas with deer access in early succession.

### Discussion

I had expected selective foraging by deer on forbs to negatively affect the overall abundance of forbs, but I saw no such effect in the early or late successional grasslands. In mid-succession, however, I did find increased abundances of forbs inside the deer exclosures, suggesting release from herbivory by deer. *Cirsium arvense* showed a substantial response to deer exclosures in my study, with increased abundances inside deer exclosures in all three

fields (Fig. 4.4). Kucera (1976) reported that this plant was a preferred forage species for white-tailed deer in Manitoba, and Marten et al. (1987) found that the nutritional content of *C. arvense* is comparable or greater to that of *Medicago sativa*, a highly nutritious legume. This supports the interpretation that higher abundances of *C. arvense* inside the deer exclosures reflected direct release from herbivore pressure that occurred outside the exclosures. Anderson et al. (2005) identified *Solidago canadensis* as an unpreferred species which increased in areas of tallgrass prairie accessible to deer. In my study, however, *S. canadensis* increased in abundance areas with and without deer access, with no difference attributable to deer (Fig. 4.5).

Because I had expected lower abundances of forbs in areas with deer access, I also expected higher abundances of grasses in those areas. I found no statistically significant difference in the overall abundance of grasses in early succession due to deer access, but by the last year, the dominant grass (*Setaria viridis*) was significantly more abundant in plots with deer access. Overall, abundance of grasses did follow the expected pattern in mid-succession, where there was a tendency for higher abundances of perennial grasses (*Bromus inermis*, *Festuca arundinacea*, and *Poa pratensis*) in control plots than inside exclosures, but not in late succession. Anderson et al. (2001) found very little browsing on grasses by deer and, perhaps because the grasses in our oldfields were different from those found in tallgrass prairies, their conclusion that foraging habits of deer favor the competitive abilities of grasses over forbs did not consistently apply to our grasslands.

Because many studies have demonstrated negative effects of deer on frequencies and abundances of woody seedlings (Inouye et al. 1994, Russell et al. 2001, Knapp et al. 2002), I expected lower abundances of woody seedlings in plots with deer access than inside the

exclosures. Two species of trees, *Prunus serotina* and *Gleditsia triacanthos*, showed strong trends with deer access in both our early and late successional grasslands (Fig. 4.3), but the patterns were opposite. They occurred in similar frequencies in the two fields, but occurred only in plots accessible to deer in early succession and, with only one exception, occurred only inside deer exclosures in late succession. These contrasting results indicate no clear effect of deer accessibility on tree seedlings in our grasslands, at least over this short time scale of 3 years.

Anderson et al. (2005) reported increased species richness, evenness, and diversity in the first few years after deer exclusion in Illinois prairies, and I had expected similar patterns in these successional old fields. However, deer have also been shown to disperse seeds of over 70 species of herbs, shrubs, and trees (Myers et al. 2004), which may increase species richness and diversity in areas with deer activity. I found no significant pattern in richness, evenness, or diversity associated with deer accessibility, although I did find a slight trend for higher species richness in areas with deer access in early succession. I frequently encountered deer pellets in the old fields and deer may have been actively dispersing seeds into the old fields, thereby compensating for their consumption of vegetation. Although I noticed no deer paths or other signs of trampling in my sampling plots, such activity could affect seedling establishment either positively, by disturbing the ground and opening light gaps, or negatively, by crushing seedlings. While many palatable, leguminous species were present in the prairies studied by Anderson et al. (2001, 2005), the only leguminous species in the my plots were *Medicago sativa* and *Trifolium pratense*. Deer may therefore have foraged less selectively on plants in these old fields.

Quantification of seed dispersal and disturbance by deer might contribute significantly to understanding the role of deer in these successional grasslands. In addition, while this short-term study identified some decreases in forb abundances and increases in graminoids with deer activity, more extensive and longer term studies probably are needed to determine their effect on less abundant forbs and woody plants.

### Literature Cited

- ANDERSON, R. C. and A. KATZ. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. *Biological Conservation* 63: 203-208.
- ANDERSON, R. C.; CORBETT, E. A., M. R. ANDERSON, G. A. CORBETT, and T. M. KELLEY. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *Journal of the Torrey Botanical Society* 128: 381-392.
- ANDERSON, R. C., D. NELSON, M. R. ANDERSON, and M. A. RICKEY. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on tallgrass prairie forbs: Diversity and species abundances. *Natural Areas Journal* 25: 19-25
- AUGUSTINE, D. J. and P. A. JORDAN. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *Journal of Wildlife Management* 62: 1076-1085.
- CONOVER, W. J.. 1980. Practical nonparametric statistics, 2nd edition. John Wiley and Sons, New York.
- CORNICELLI, L., A. WOOLF, and J. L. ROSEBERRY. 1996. White-tailed deer use of a suburban environment in southern Illinois. *Transactions of the Illinois State Academy of Science* 89:93-103.
- CRITICAL TRENDS ASSESSMENT PROGRAM (CTAP). 2001. Critical trends in Illinois Ecosystems. Illinois Department of Natural Resources. Accessed at <http://dnr.state.il.us/orep/ctap2/TOC.pdf>
- GILL, R. M. and V. BEARDALL. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:209-218.

- ILLINOIS DEPARTMENT OF ENERGY AND NATURAL RESOURCES (IDENR). 1994. The Changing Illinois Environment: Critical Trends. Summary Report and Volumes 1-7 Technical Report. Illinois Department of Energy and Natural Resources, Springfield, IL, ILENR/RE-EA-94/05.
- INOUE, R. S., T. D. ALLISON, and N. C. JOHNSON. 1994. Old field succession on a Minnesota sand plain: Effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club* 121:266-276.
- KNAPP, A. K., J. M. BRIGGS, J. BOKDAM, and D. J. VAN DER HOEK. 2002. White-tailed deer browsing on six shrub species of tallgrass prairie. *Great Plains Research* 12(1): 141-156.
- KREBS, C. J. 1999. *Ecological methodology*. 2nd ed. Benjamin/Cummings, Menlo Park, California.
- KUCERA, E.. 1976. Effects of winter conditions on the white-tailed deer of Delta Marsh, Manitoba. *Canadian Journal of Zoology* 54: 1307-1313.
- MARTEN, G. C., C. C. SHEAFFER, and D. L. WYSE. 1987. Forage nutritive value and palatability of perennial weeds. *Agronomy Journal* 79: 980-986.
- MOHLENBROCK, R. H.. 2002. *Vascular Flora of Illinois*. Southern Illinois University Press.
- MYERS, J. A., M. VELLEND, S. GARDESCU, and P. L. MARKS. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139: 35-44.
- NIXON, C. M., L. P. HANSEN, P. A. BREWER, J. E. CHELSVIG, T. L. ESKER, D. ETTER, J. B. SULLIVAN, R. G. KOERKENMEIER, and P. C. MANKIN. 2001. Survival of white-tailed deer in intensively farmed areas of Illinois. *Can. J. of Zoology* 79: 581-588.
- ROONEY, T. P. and D. M. WALLER. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*. 181: 165-176.
- RUSSELL, F. L., D. B. ZIPPEN, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. *American Midland Naturalist* 146: 1-26.
- WALLER, D. M. and W. S. ALVERSON. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25:217-226.
- ZAR, J. H.. 1996. *Biostatistical analysis*. Prentice-Hall.

Figure 4.1. Mean ( $\pm 1 SE$ ) relative abundances of forbs in A) early succession, B) mid-succession, and C) late succession. Means across 3 replicates in May (M), July (J), and September (S). No data were collected in May 2003 for early succession.

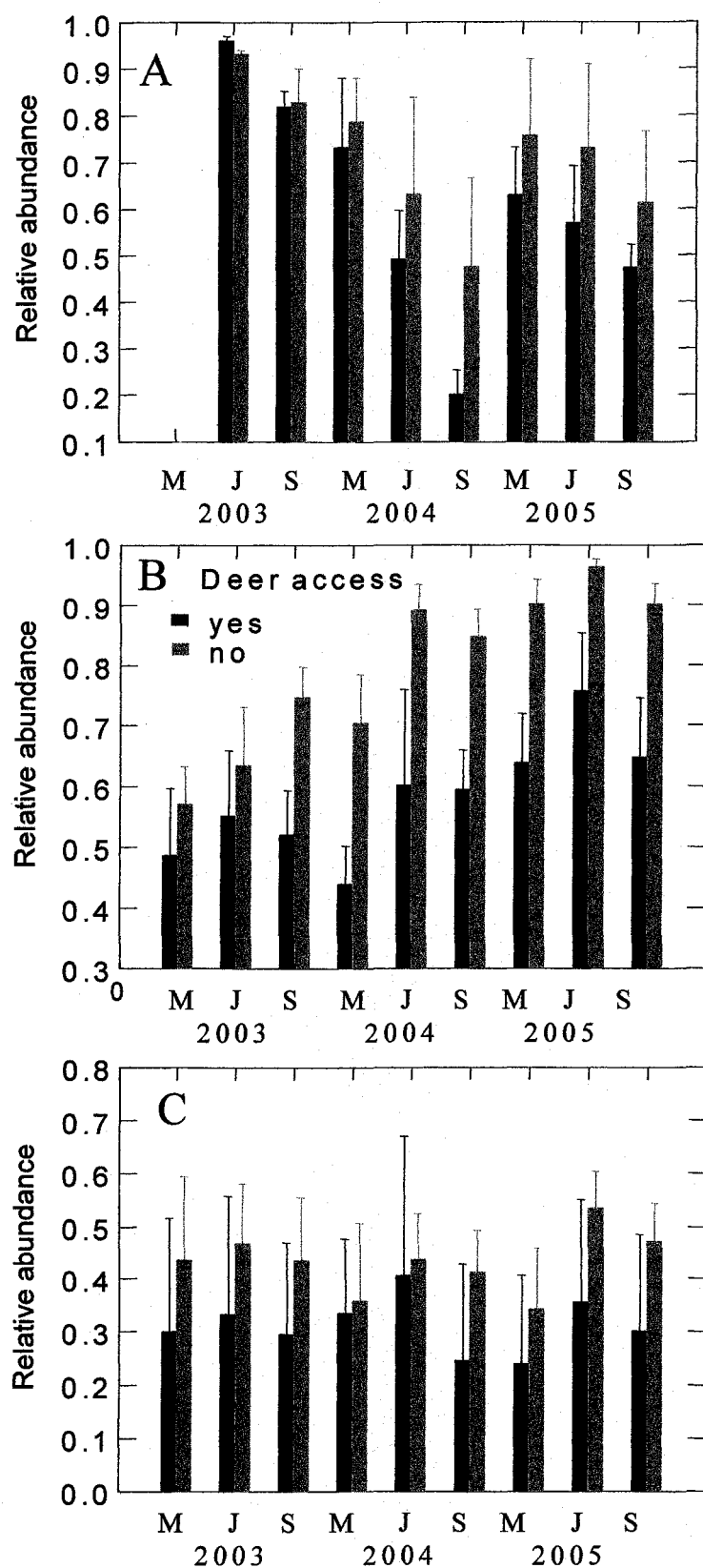


Figure 4.2. Mean ( $\pm 1$  SE) relative abundances of the dominant grasses (*Setaria viridis* in early succession and *Festuca arundinacea* in mid and late succession) in A) early succession, B) mid-succession, and C) late succession. Means across 3 replicates in May (M), July (J), and September (S). No data were collected in May 2003 for early succession.

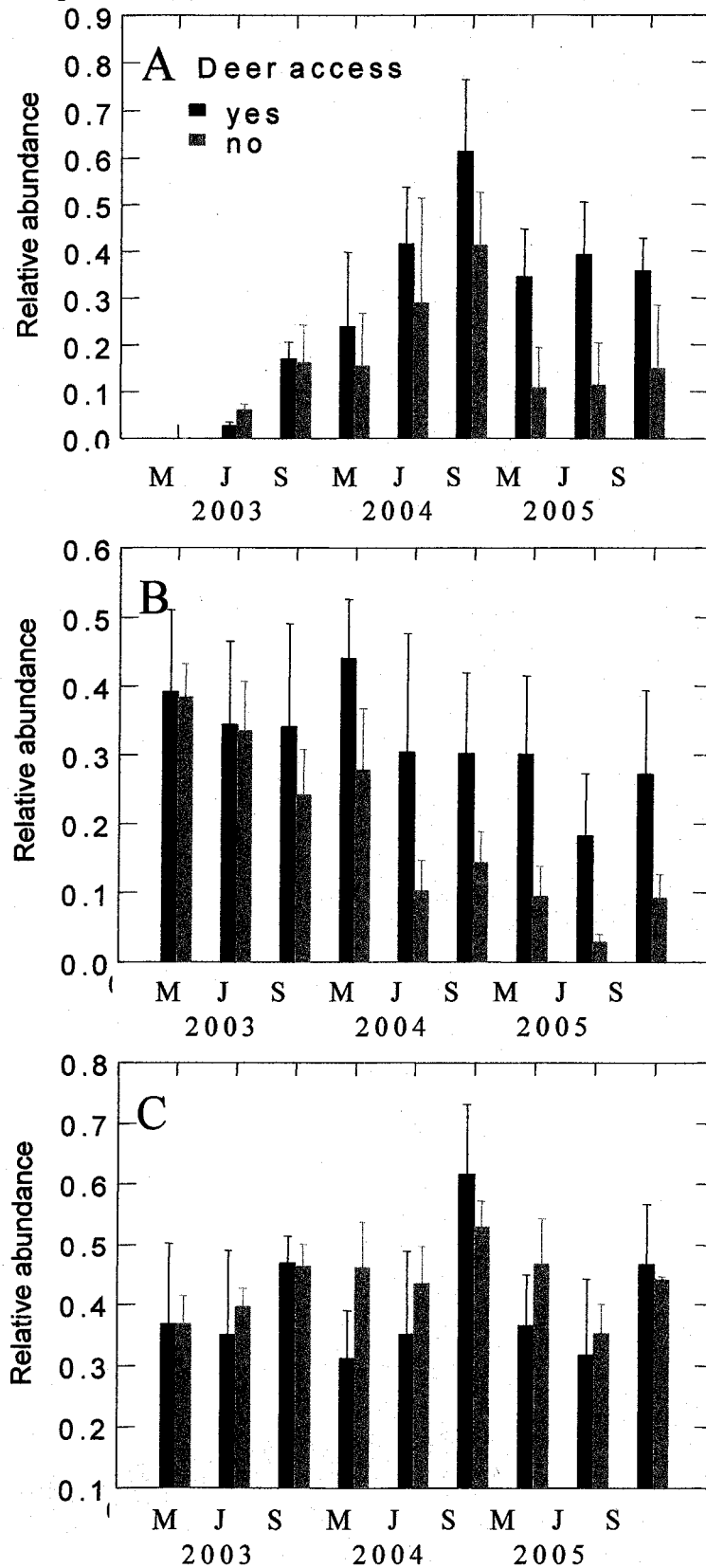




Figure 4.3. Means ( $\pm 1 SE$ ) for *Gleditsia triacanthos* in A) early succession and B) late succession and for *Prunus serotina* in C) early succession and D) late succession. Means across 3 replicates in May (M), July (J), and September (S). No data were collected in May 2003 for early succession.

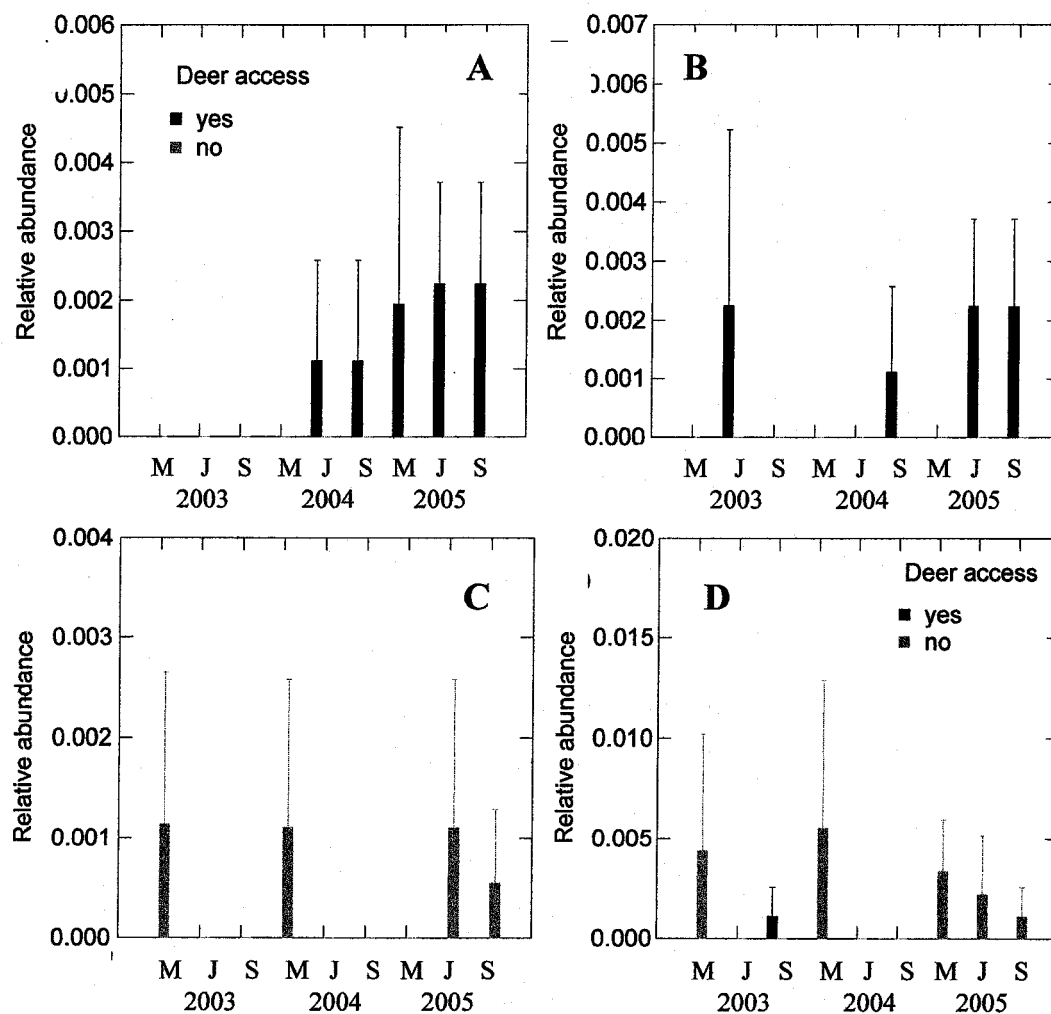


Figure 4.4. Means ( $\pm 1$  SE) for *Cirsium arvense* in A) early succession, B) mid-succession, and C) late succession. Means across 3 replicates in May (M), July (J), and September (S). No data were collected in May 2003 for early succession.

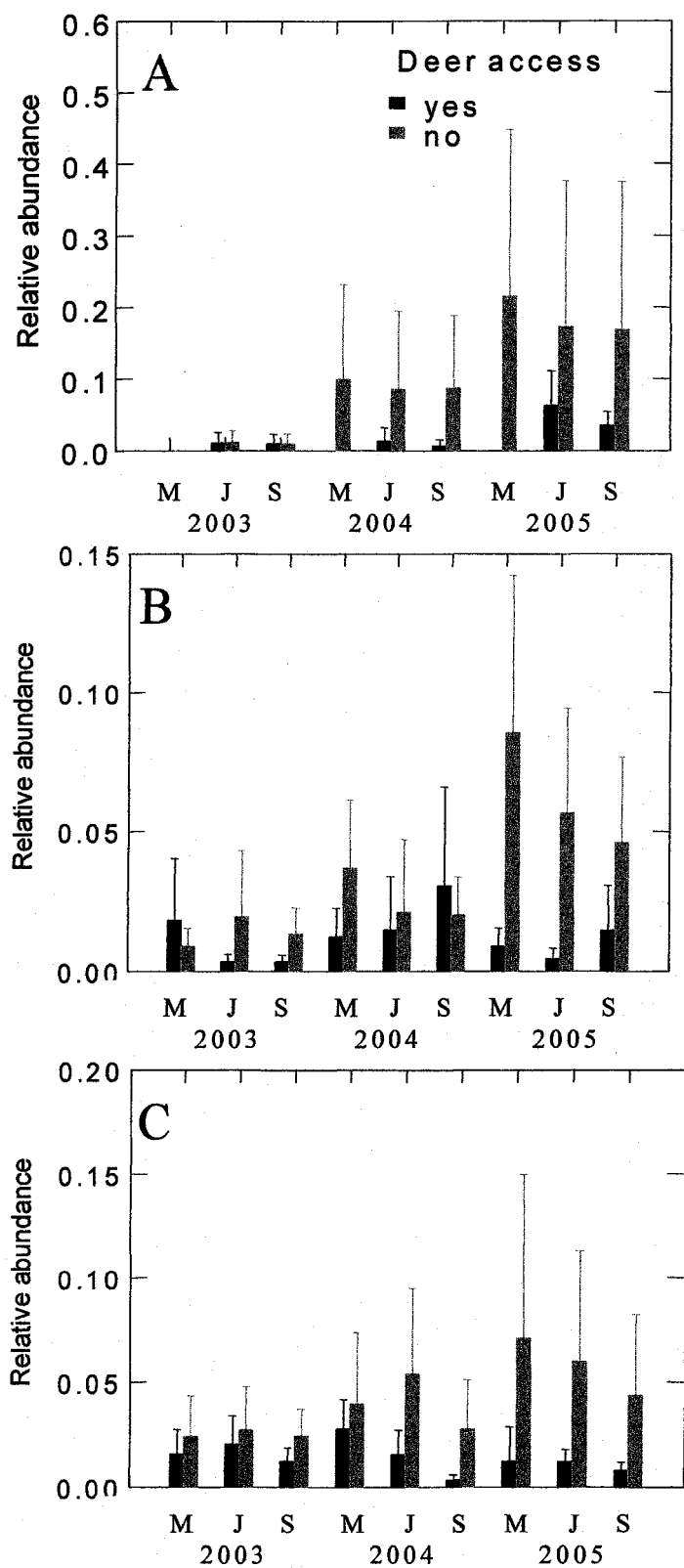
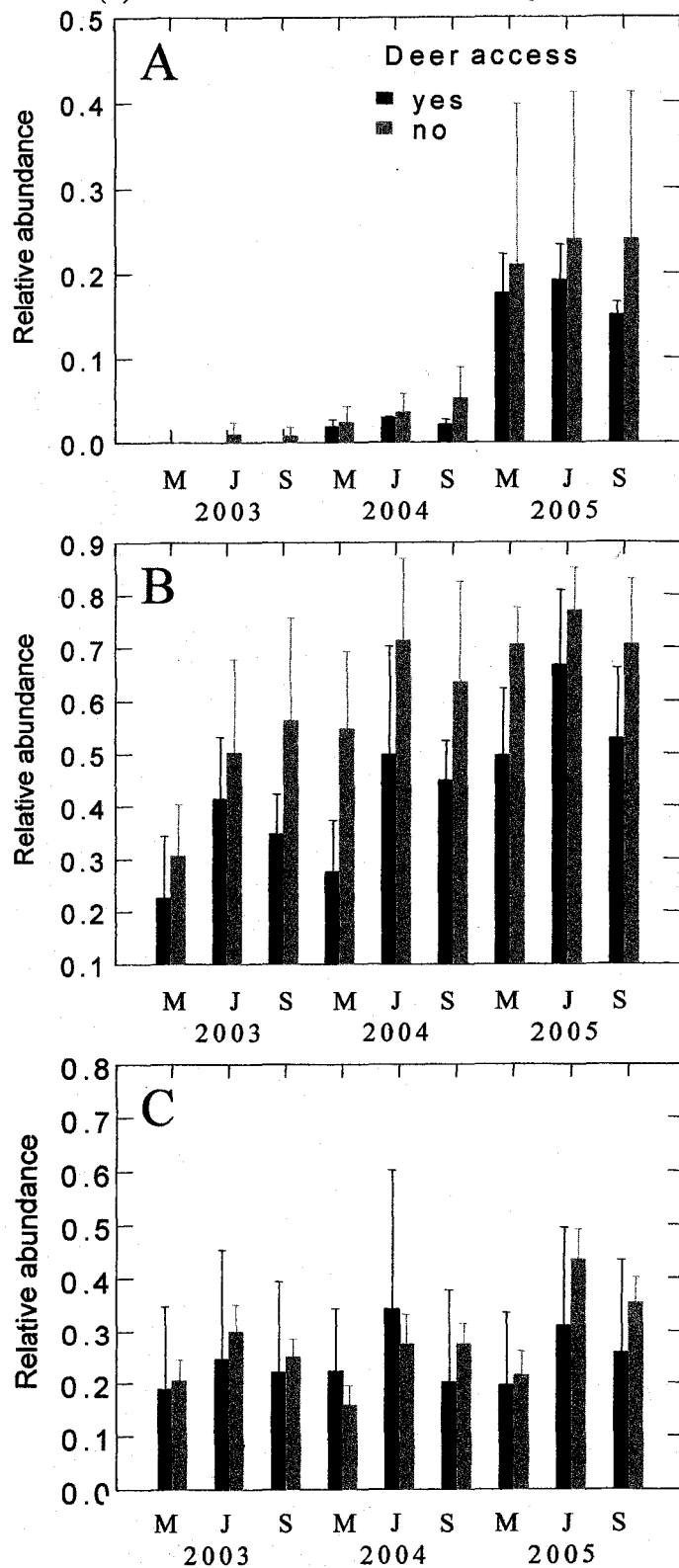


Figure 4.5. Means ( $\pm 1 SE$ ) for *Solidago canadensis* in A) early succession, B) mid-succession, and C) late succession. Means across 3 replicates in May (M), July (J), and September (S). No data were collected in May 2003 for early succession.



## CHAPTER 5

### CONCLUSIONS

I designed this study to examine the ways in which mammalian herbivores and granivores influence the development of old-field grasslands. Here I compare the mechanisms and contributions of the different mammal types to assess the overall effect of mammals and to place my results in the context of previous work on mammalian herbivores in grasslands.

I found no effect of endozoochory by rabbits on plant communities in any successional stage. While many plant species did germinate from rabbit fecal pellets, any effect of endozoochory appeared overwhelmed by the impact of herbivory. The low importance of seed dispersal by rabbits mimicked results found in western rangelands (Schupp et al. 1997). While studies in European grasslands have shown important contributions of endozoochorous dispersal by rabbits to the seed bank (Malo et al. 1995, 1996; Pakeman et al. 1998a, 1998b), these were annual grasslands with domestic grazers (greater disturbance) and higher densities of rabbits.

Deer may also disperse seeds in their feces (Gill and Beardall 2001, Myers et al. 2004). While red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) disperse at least 60 different species of plants in Europe, studies of seed dispersal by the white-tailed deer (*Odocoileus virginianus*) in the U.S.A. have concluded that herbivory by deer is more influential on plant communities than seed dispersal (Ruhren and Handel 2003, Furedi and McGraw 2004). Endozoochory by deer was not investigated here, and I found no indication

of deer endozoochory influencing these plant communities (no decrease in species richness or diversity in the absence of deer).

I found no clear preference of rodents for large seeds and no effect of rodents on large-seeded plants in any stage of succession, not even in early succession, where I expected granivory to strongly affect recruitment into the plant community. This result contrasted with many studies in which granivory by rodents significantly influenced plant community composition. Brown and Heske (1990) and Samson et al. (1992) both reported increases in large-seeded annuals when rodents were excluded from areas of Chihuahuan desert, Hoffmann et al. (1995) reported more seed foraging by rodents on larger seeds in Colorado shortgrass steppe, Howe and Brown (1999, 2000) found fewer large-seeded plants in prairie plantings with rodent access, and Hulme (1994) identified rodents as major seed consumers in grasslands of the U.K.. Rodents in my study consumed a wide variety of seeds, so overall seed predation distributed across numerous species had little effect on the plant community.

Reports of little effect of rodent granivory on vegetation often refer to greater effects of ants or birds. Vasquez et al. (1995) reported little influence of rodents in the Chilean matorral, where ants were the most important seed predator, and birds had intermediate influence. Reader and Beisner (1999) found neither rodents nor birds decreased seedling emergence in old fields of Ontario, although ants did. A preliminary report from one ant and rodent exclusion study in the Sonoran desert reported that ants and rodents competed for seeds of similar sizes, each compensating when the other was removed (Brown and Davidson 1977). A later paper, however, clarified that rodent removals resulted in increased abundances of large-seeded plants and decreased abundances of small-seeded plants while ant removal resulted in the opposite pattern (Davidson et al. 1984). Ant-rodent-seed

interactions were a bit more complicated in the Chihuahuan desert, where granivory by ants and rodents had compensatory effects on winter annuals, but not summer annuals (Davidson et al. 1985). Harvesting of seeds by ants has not, to my knowledge, been studied in Illinois grasslands but seed removal by ants could be another mechanism by which plant communities are influenced.

Seed predation may play only a minor role in community succession and maintenance if plants generate primarily by vegetative means (as *S. canadensis* does) or if seed losses to predation are small relative to the seed bank (Hulme 1996). I had assumed that by mid- and late succession, when perennial plants were common, recruitment of shoots by rhizomes would be more important than seeds. In contrast, I expected that in early succession, seed dispersal by rabbits and loss of large seeds to rodents would more heavily influence plant recruitment. But I found neither mechanism operating in early succession. In addition, I expected significantly fewer annual plants in areas with access by herbivores and granivores in early succession. Batzli and Pitelka (1970) had reported that voles reduced both relative abundances of the palatable annual plants and reduced the production of seeds in annual grasslands in California, but I saw no response of annual plants to exclusion of any type of mammal.

Herbivory by each group of mammals showed some impact on the plant community. For instance, herbivory in general reduced the abundance of palatable forbs which, in turn, resulted in higher abundance of unpalatable forbs. This effect was hardly seen in late succession, however, due to the few palatable plants in this field that had been exposed to herbivory for many years prior to this study. Goldenrod, highly palatable to rabbits in spring, had significantly lower abundance on plots with access by rabbits in all fields. In contrast,

higher abundance of goldenrod occurred in plots with rodent access than without, and voles showed that they found goldenrod unpalatable. Two other studies of vole herbivory in tallgrass prairies found increased goldenrod biomass outside of vole exclosures (Weis 1975) and with higher vole populations (Gibson et al. 1990). Anderson et al. (2005) determined that goldenrod was unpalatable to deer, resulting in a positive effect of deer on its growth and abundance in tallgrass prairie remnants, but I saw no effect of deer.

In Mediterranean grasslands of Israel, high vole populations resulted in the disappearance of tall annual grasses and one dominant perennial (*Hordeum bulbosum*), which were replaced by unpalatable annual crucifers and thistle (Noy-Meir 1988). While I did notice an increase in abundance of *Barbarea vulgaris* (an unpalatable crucifer) in my mid-successional grassland at high vole densities, high variability among replicates prevented statistical significance.

Three species of palatable plants (chickweed, black nightshade, and witchgrass) that germinated from fecal pellets occurred only in plots without rabbits in early succession. These plants were all highly palatable to rabbits and unpalatable to voles. In late succession, I had trapped only a few rabbits, but 2 unpalatable forbs (wild parsnip and Canada thistle) had lower abundance in areas without rabbit access than in areas with access. While rabbit herbivory can negatively affect some species of thistle, several additional studies indicate that rabbits positively affect Canada thistle (*Cirsium arvense*) by preferentially foraging on other species (van Leeuwen 1983, Palmisano and Fox 1997, Edwards et al. 2000). Kucera (1976) reported Canada thistle as a preferred forage species for white-tailed deer in Manitoba, however, and it increased significantly in abundance inside deer exclosures at all

stages of succession. Weis (1975) found greater biomass of Canada thistle inside vole exclosures, but I found no effect of voles on this plant.

Alfalfa (*Medicago sativa*), a forb with highly palatable seeds and shoots received a one-two punch by the rodents and declined more rapidly in the mid-successional field where exposed to rodents than where protected from them. Neither deer nor rabbits had a significant effect on this plant.

While changes in the overall relative abundance of forbs would necessarily result in changes in relative abundances of graminoids (nearly all plants were one or the other), responses of individual forb species did not always correspond with a change in graminoids. In spite of all grasses being at least moderately palatable to rabbits, I found no effect of rabbits on the abundance of graminoids. I had expected no influence of herbivory on graminoids due to their more protected basal meristems, but my results do contrast with those of Watt (1962) and Sumption and Flowerdew (1985), who overall found increased abundances of *Festuca*, *Poa*, and *Dactylis* in areas with reduced rabbit access in the United Kingdom. Those grasslands, however, had had severe grazing by very high densities of rabbits. Plots without deer access, on the other hand, had lower relative abundances of *Festuca arundinacea* in mid-succession than the plots to which deer had access, which reflected higher abundance of Canada thistle. With vole exclusion, the overall abundance of grasses palatable to voles (*Festuca arundinacea*, *Lolium perenne*, *Dactylis glomerata*, and *Bromus inermis*) increased in both the mid- and late successional fields.

Bluegrass (*Poa pratensis*), which had palatable seeds but relatively unpalatable shoots, accounted for increased abundance of palatable-seeded plants with rodent access in late succession, probably a response to reduced abundance of palatable graminoids



(competitive release). I found no such effect in mid-succession, however. These results contrast with reports of decreased abundances of *P. pratensis* with *M. pennsylvanicus* in grasslands where *P. pratensis* constituted up to 99% of the total standing biomass (Weis 1975) and in tallgrass prairies with high population densities of *M. ochrogaster* (Gibson et al. 1990). Prairie voles (*M. ochrogaster*) will take large amounts of bluegrass when it has high availability even though its nutrition cannot sustain them (Cole and Batzli 1979). This suggests that voles had fewer high quality food items to choose from in tallgrass prairie, making *P. pratensis* a more attractive food item for voles there than in my old fields. Dusi (1952) ranked bluegrass as an important food for rabbits, but it scored poorly in my palatability trials, and I detected no effect by rabbits.

I found no effect of any mammal group on woody seedlings in any successional stage, contrary to many published studies that have shown negative effects of voles, rabbits, and deer on the establishment of woody plants in grasslands (see citations in previous chapters, particularly Pusenius et al. 2000, Manson et al. 2001). Because I rarely encountered woody seedlings in my fields, the location and scale of my study appeared inappropriate to detect such effects.

Crawley (1983) suggested that the main effect of herbivores on diversity of the plant community would be not through extermination of palatable species (directly affecting species richness), but by simply modifying the competitive abilities of the plant species. If herbivores caused decreased relative abundances of dominant species, this would result in higher species evenness, whereas if they foraged on less common species, evenness of the plant community would decrease. In my grasslands, however, individual types of mammals had relatively small effects on species richness, evenness, or diversity and only in some fields

(largest effects were evenness and diversity 2x higher without rodent access in mid-succession in 2004). When I analyzed the response of the plant communities to all small mammals (mice, voles, rabbits), however, substantial differences due to mammal access emerged in early and mid-succession.

Using RM-ANOVA, I compared the plots to which only deer had access (no small mammals) and the plots to which all animals had access (false exclosures). I found a significant response of species richness to exclusion of small mammals, with lower richness in exclosures ( $P=0.075$ ) and a stronger effect (25-45% less) in the last year of data collection (treatment X year,  $P=0.055$ ; Fig. 5.1a). No consistent trend in species evenness occurred in response to the treatment (Fig. 5.1b). Overall species diversity remained 23-38% lower in the exclosures during the last year of the study (treatment X year,  $P=0.071$ ; Fig. 5.1c).

In mid-succession, analysis indicated a significant interaction between small animal access and season ( $P=0.006$ ) in species richness (Fig. 5.2a). In spring, richness was higher outside the exclosures (due to unpalatable spring annuals, such as *Thlaspi arvense*) while later in the year, the opposite was true. Species evenness was greater inside exclosures but this pattern had been present since the start of the experiment and the difference was marginally insignificant ( $P=0.126$ ; Fig. 5.2b). Species diversity responded to overall small mammal exclusion in a pattern similar to that for evenness, but the difference between the treatments increased over time, resulting in greater diversity in exclosures, although non-significant ( $P=0.146$ ; Fig. 5.2c). Although factors of year and season were both significant ( $P<0.10$ ), there were no interactions with treatment ( $P>0.25$ ).

In late succession, a significant interaction developed between small mammal access and year for species richness ( $P=0.094$ ; Fig. 5.3a). At the beginning and end of the study,

more species occurred outside exclosures, but in 2003, more were present inside the exclosures. Species evenness also showed a significant treatment X year interaction ( $P=0.089$ ; Fig. 5.3b). In this case, evenness was higher outside the exclosures in 2002, showed the opposite pattern in the second year, and no pattern in the third year. Because species richness and evenness showed opposite trends, there were no significant differences in overall diversity. When looking only at the effect of rabbits in this grassland, higher plant diversity occurred in plots without rabbits, reflecting a trend for higher richness and evenness in areas without rabbit herbivory. Thus, the effects of rodents and rabbits appeared to counteract one another in late succession.

Overall effects of seed consumption and endozoochory appeared quite small and generally overshadowed by herbivory. While effects of mammals on individual species of plants frequently occurred, the overall effect was to increase species diversity by the third year of succession, to reduce it by year 6 or 7, but to have little effect by year 15. It is possible that exclusion of mammals over longer periods of time would intensify effects and lead to more substantial changes in the plant community.

Although I attempted to investigate influences of herbivores over a longer period by using old fields at three stages of succession, still, I only maintained the experiment for 3 to 3 1/2 years in each field. In the early successional grassland, differences seemed to be emerging, but in the late successional grassland, the “ghosts of herbivory past” may have left a lasting impression. Very low abundances of highly palatable forbs occurred there, some of which just began to appear inside the exclosures in the last year of this study. Perhaps the “ghosts” just began to fade. Clearly, a longer study is needed before concluding that mammals only have transient effects on these grasslands.

### Literature Cited

- ANDERSON, R. C. and A. J. KATZ. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure. *Biological Conservation* 63: 203-208.
- ANDERSON, R. C., D. NELSON, M. R. ANDERSON, and M. A. RICKEY. 2005. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on tallgrass prairie forbs: Diversity and species abundances. *Natural Areas Journal* 25: 19-25.
- BATZLI, G. O. and F. A. PITELKA. 1970. Influence of meadow mouse populations on California grasslands. *Ecology* 51: 1027-1039.
- BROWN, J. H. and D. W. DAVIDSON. 1977. Competition between seed eating rodents and ants in desert ecosystems. *Science* 196: 800-882.
- BROWN, J. H. and E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- COLE, F. R. and G. O. BATZLI. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. *Journal of Animal Ecology* 48: 455-470.
- CONOVER, W. J.. 1980. Practical nonparametric statistics, 2nd edition. John Wiley and Sons, New York.
- DAVIDSON, D. W.. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23-35.
- DAVIDSON, D. W., R. S. INOUE, and J. H. BROWN. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65: 1780-1786.
- DAVIDSON, D. W., D. A. SAMSON, and R. S. INOUE. 1985. Granivory in the Chihuahuan desert USA: interactions within and between trophic levels. *Ecology* 66: 486-502.
- De STEVEN, D.. 1991. Experiments on mechanics of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72: 1076-1088.
- DUSI, J. L.. 1952. The food habits of several populations of cottontail rabbits in Ohio. *J. Wildlife Man.* 16: 180-186.
- EDWARDS, G. R. and M. J. CRAWLEY. 1999. Effects of disturbance and rabbit grazing on seedling recruitment of six mesic grassland species. *Seed Science Research* 9: 145-156.

- EDWARDS, G. R., G. W. BOURDOT, and M. J. CRAWLEY. Influence of herbivory, competition, and soil fertility on the abundance of *Cirsium arvense* in acid grassland. *J. of Applied Ecology* 37: 321-334.
- FUREDI, M. A. and J. B. MCGRAW. 2004. White-tailed deer: Dispersers or predators of American ginseng seeds? *American-Midland-Naturalist*. 152: 268-276.
- GIBSON, D. J., C. C. FREEMAN, and L. C. HURLBERT. 1990. Effects of small mammals and invertebrate herbivory on plant species richness and abundances in tallgrass prairie. *Oecologia* 84: 169-175.
- GILL, D. S. and P. L. MARKS. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monographs* 61: 183-205.
- GILL, R. M. A. and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:209-218.
- HAKEN, A. E. and G. O. BATZLI. 1996. Effects of availability of food and interspecific competition on diets of prairie voles (*Microtus ochrogaster*). *J. Mamm.* 77: 315-324.
- HOFFMANN, L. A., E. F. REDENTE, and L. C. McEWEN. 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecol. Appl.* 5: 200-208.
- HOWE, H. F. and J. S. BROWN. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776-1781.
- HOWE, H. F. and J. S. BROWN. 2000. Early effects of rodent granivory on experimental forb communities. *Ecological Applications* 10: 917-924.
- HOWE, H. F. and J. S. BROWN. 2002. The ghost of granivory past. *Ecology Letters* 4: 371-378.
- HULME, P. E.. 1994. Post-dispersal seed predation in a grassland: its magnitude and sources of variation. *J. of Ecology* 82: 645-52.
- INOUE, R. S., T. D. ALLISON, and N. C. JOHNSON. 1994. Old field succession on a Minnesota sand plain: Effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club*. 121: 266-276.
- KUCERA, E.. 1976. Effects of winter conditions on the white-tailed deer of Delta Marsh, Manitoba. *Canadian Journal of Zoology* 54: 1307-1313.
- LINDROTH, R. L. and G. O. BATZLI. 1984. Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. *J Mamm* 65: 600-606.

- MALO, J. E., and F. SUAREZ. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104:246-55.
- MALO, J. E., and F. SUAREZ. 1996. New insights into pasture diversity: the consequences of seed dispersal in herbivore dung. *Biodiversity Letters* 3:54-57.
- MANSON, R. H.. 2000. Spatial autocorrelation and the interpretation of patterns of tree seed and seedling predation by rodents in old-fields. *Oikos* 91: 162-174.
- MANSON, R. H., R. S. OSTFELD, and C. D. CANHAM. 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* 82: 3320-29.
- MARTEN, G. C., C. C. SHEAFFER, and D. L. WYSE. 1987. Forage nutritive value and palatability of perennial weeds. *Agronomy Journal* 79: 980-986.
- MYERS, J. A., M. VELLEND, S. GARDESCU, and P. L. MARKS. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139:35-44.
- NOY-MEIR, I.. 1988. Dominant grasses replaced by ruderal forbs in a vole year in undergrazed Mediterranean grasslands in Israel. *J. Biogeogr.* 15: 579-587.
- OSTFELD, R. S. and C. D. CANHAM. 1993. Effects of meadow vole population density of tree seedling survival in old fields. *Ecology* 74: 1792-1801.
- OSTFELD, R. S., R. H. MANSON, and C. D. CANHAM. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1531-1542.
- PAKEMAN, R. J., J. P. ATWOOD, and J. ENGELEN. 1998a. Sources of plants colonizing experimentally disturbed patches in an acidic grassland in eastern England. *Journal of Ecology* 86:1032-41.
- PAKEMAN, R. J., J. ENGELEN, and J. P. ATWOOD. 1998b. Rabbit endozoochory and seedbank build-up in an acidic grassland. *Plant Ecology* 145: 83-90.
- PALMISANO, S. and L. R. FOX. 1997. Effects of mammal and insect herbivory on population dynamics of a native Californian thistle, *Cirsium occidentale*. *Oecologia* 111: 413-421.
- PUSENIUS, J. and R. S. OSTFELD. 2000. Effects of stoats presence and auditory cues indicating its presence on tree seedling predation by meadow voles. *Oikos* 91: 123-130.
- PUSENIUS, J., R. S. OSTFELD, and F. KEESING. 2000. Patch selection and tree-seedling predation by resident and immigrant meadow voles. *Ecology* 81: 2951-2956.

- READER, R. J. and B. E. BEISNER. 1991. Species-dependent effects of seed predation and ground cover on seedling emergence of old-field forbs. *Am. Midl. Nat.* 126: 279-286.
- RUHREN, S. and S. N. HANDEL. 2003. Herbivory constrains survival, reproduction and mutualisms when restoring nine temperate forest herbs. *Journal of the Torrey Botanical Society.* 130: 34-42.
- SAMSON, D. A., T. E. PHILIPPI, D. W. DAVIDSON. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos* 65:61-80.
- SCHUPP, E. W., H. J. HEATON, and J. M. GOMEZ. 1997. Lagomorphs and the dispersal of seeds into communities dominated by exotic annual weeds. *Great Basin Naturalist* 57: 253-58.
- SUMPTION, K. J. and J. R. FLOWERDEW. 1985. The ecological effects of the decline of rabbits (*Oryctolagus cuniculus*) due to myxomatosis. *Mammal Review* 15: 151-86.
- TANSLEY, A. G., and R. S. ADAMSON. 1925. Studies of the vegetation of the English chalk. *Journal of Ecology* 13:177-223.
- VAN LEEUWEN, B. H.. 1983. The consequences of predation in the population biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare*. *Oecologia* 58: 178-187.
- VASQUEZ, R. A., R. O. BUSTAMANTE, and J. A. SIMONETTI. 1995. Granivory in the Chilean matorral: extending the information on arid zones of South America. *Ecography* 18: 403-409.
- WATT, A. S. 1962. The effect of excluding rabbits from Grassland A (Xerobrometum) in Breckland, 1936-1960. *Journal of Ecology* 50: 181-198.
- WEIS, I. M.. 1975. Alterations in a grassland plant community: the effects of microtine herbivory. Ph. D. dissertation, University of Iowa.
- ZIMMERMAN, E. G. 1965. A comparison of habitat and food of two species of *Microtus*. *J. Mamm.* 46: 605-12.

Figure 5.1. Mean ( $\pm 1 SE$ ) for A) species richness, B) species evenness, and C) Gini coefficient of diversity comparing plots with access by all small mammals and no small mammals in early succession in July (J), September (S), and May (M), 2002 to 2005.

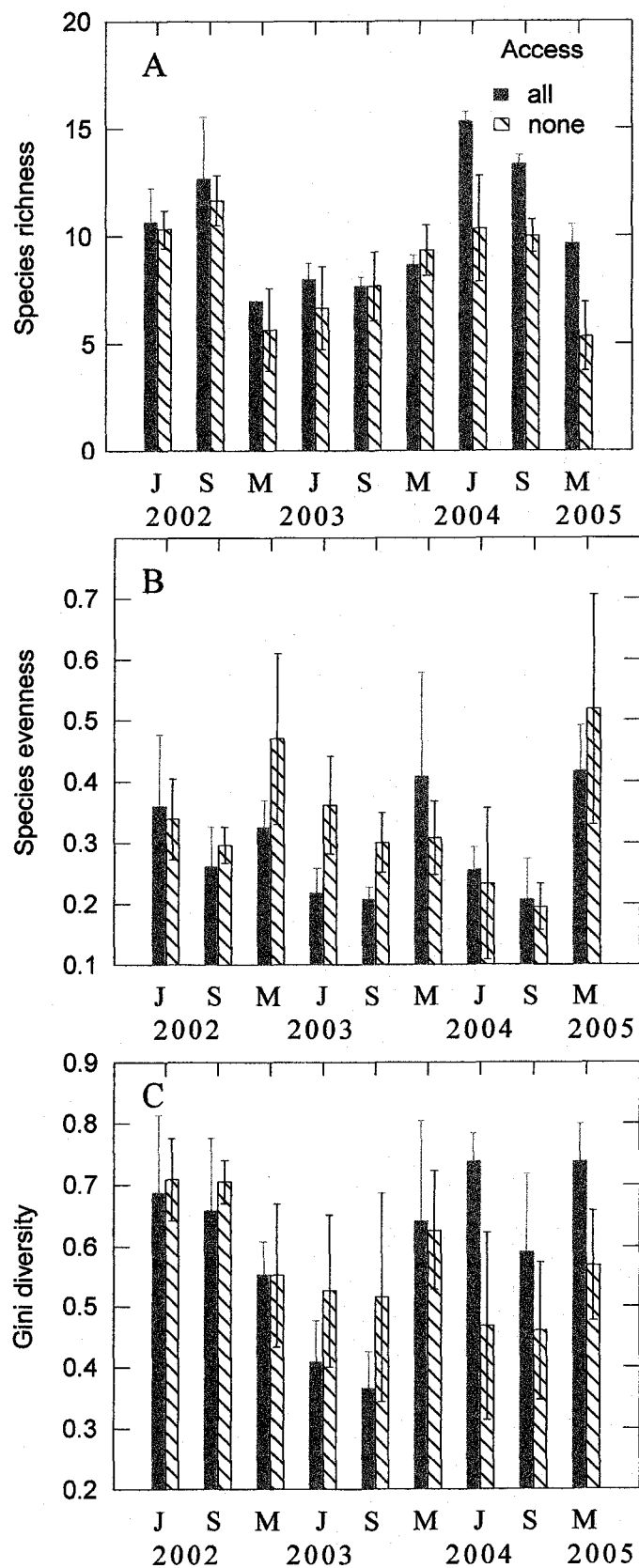




Figure 5.2. Mean ( $\pm 1 SE$ ) for A) species richness, B) species evenness, and C) Gini coefficient of diversity comparing plots with access by all small mammals and no small mammals in mid-succession in September (S), May (M), and July (J), 2001 to 2005.

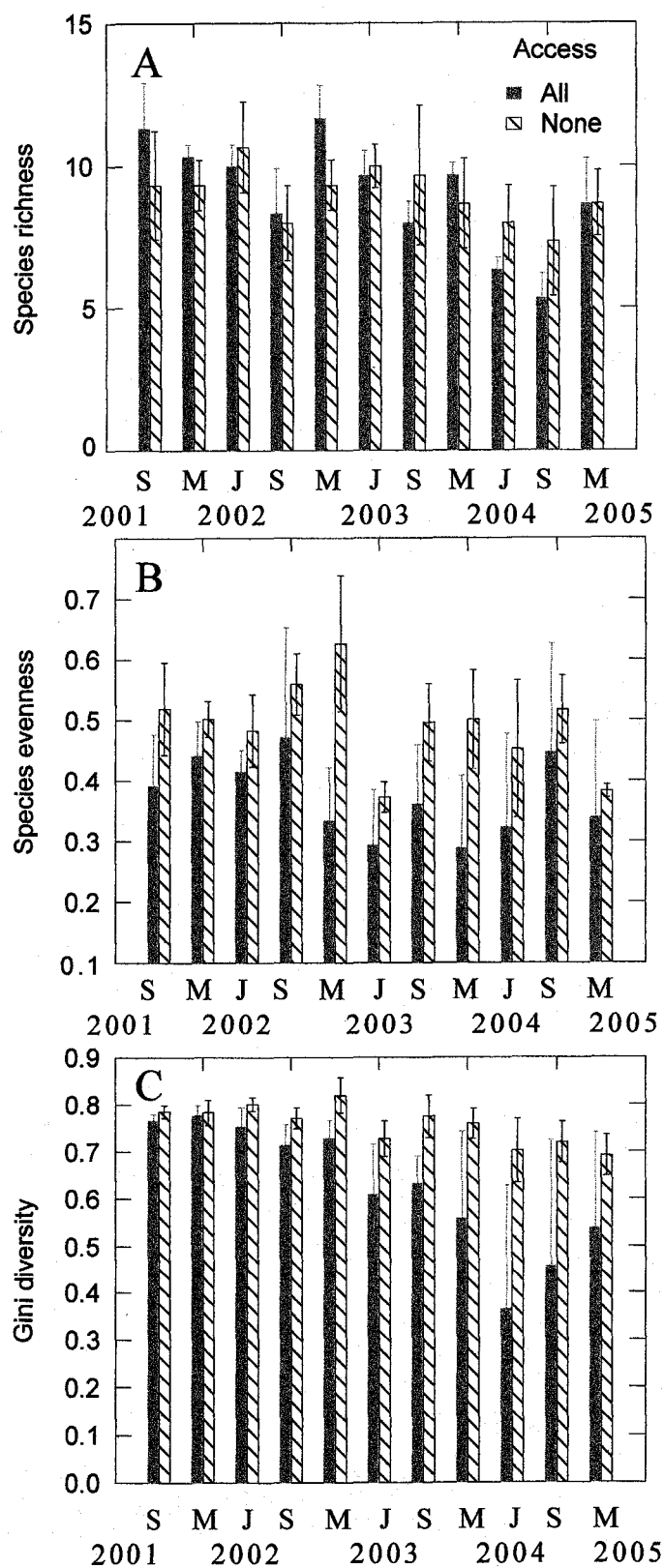
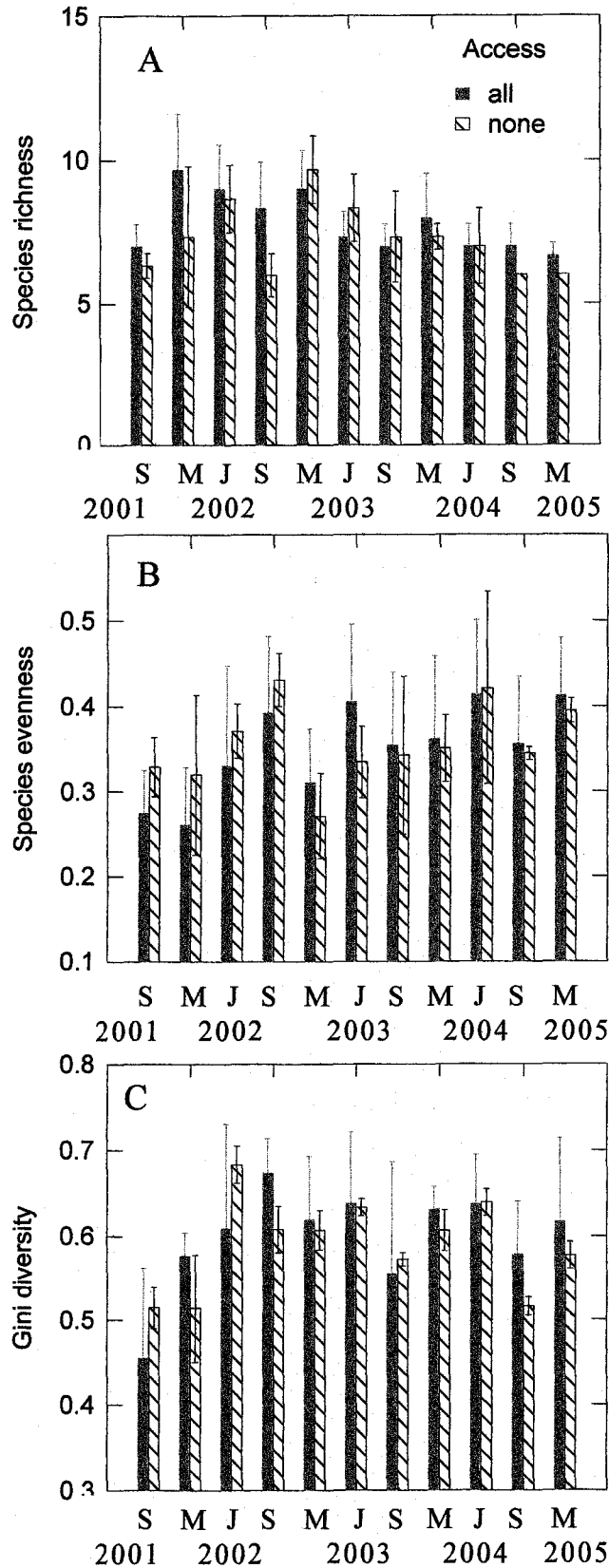


Figure 5.3. Mean ( $\pm 1 SE$ ) for A) species richness, B) species evenness, and C) Gini coefficient of diversity comparing plots with access by all small mammals and no small mammals in late succession in September (S), May (M), and July (J), 2001 to 2005.



## APPENDIX A.

Statistical tables for repeated measures ANOVA testing hypotheses regarding rabbit access in 1) early succession, 2) mid-succession, and 3) late succession.

## 1. Early succession

## Rabbit-dispersed plants

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	3.130	1	3.130	1.536	0.283		
Error	8.148	4	2.037				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	1.037	2	0.519	0.080	0.924	0.869	0.924
Error	51.852	8	6.481				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	4.148	2	2.074	0.855	0.461	0.413	0.440
Error	19.407	8	2.426				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	3.852	4	0.963	0.241	0.911	0.814	0.911
Error	63.926	16	3.995				

## Rabbit-dispersed forbs

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	9.796	1	9.796	0.629	0.472		
Error	62.259	4	15.565				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	1.926	2	0.963	0.342	0.720	0.672	0.720
Error	22.519	8	2.815				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	2.815	2	1.407	0.847	0.464	0.414	0.441
Error	13.296	8	1.662				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	2.963	4	0.741	0.383	0.817	0.633	0.740
Error	30.926	16	1.933				

## Rabbit-dispersed graminoids

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	2.250	1	2.250	0.220	0.663		
Error	40.833	4	10.208				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	2.167	2	1.083	0.164	0.852	0.815	0.852
Error	53.000	8	6.625				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	1	0.000	0.000	1.000	.	.

season*TRMT\$	0.250	1	0.250	0.857	0.407	.	.
Error	1.167	4	0.292				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.167	2	0.083	0.143	0.869	0.739	0.814
Error	4.667	8	0.583				

### Annual plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.296	1	0.296	0.049	0.836
Error	24.148	4	6.037		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	14.926	2	7.463	1.494	0.281	0.286	0.281
Error	39.963	8	4.995				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	3.370	2	1.685	0.636	0.554	0.499	0.554
Error	21.185	8	2.648				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	4.074	4	1.019	0.417	0.794	0.678	0.794
Error	39.037	16	2.440				

### Small-seeded plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	5.352	1	5.352	0.511	0.514
Error	41.926	4	10.481		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	4.593	2	2.296	0.360	0.708	0.607	0.683
Error	50.963	8	6.370				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.593	2	0.296	0.264	0.774	0.705	0.774
Error	8.963	8	1.120				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	13.630	4	3.407	1.732	0.192	0.242	0.192
Error	31.481	16	1.968				

### Small-seeded graminoids (summers, falls only)

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	13.444	1	13.444	1.360	0.308
Error	39.556	4	9.889		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	5.556	2	2.778	0.563	0.590	0.527	0.590
Error	39.444	8	4.931				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	1	0.000	0.000	1.000	.	.
season*TRMT\$	1.778	1	1.778	8.000	0.047	.	.
Error	0.889	4	0.222				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.222	2	0.111	0.216	0.810	0.787	0.810
Error	4.111	8	0.514				

### Small-seeded forbs

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.019	1	0.019	0.002	0.970
Error	45.926	4	11.481		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	3.704	2	1.852	0.519	0.614	0.546	0.614
Error	28.519	8	3.565				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	3.704	2	1.852	0.465	0.644	0.562	0.633
Error	31.852	8	3.981				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	4.741	4	1.185	0.486	0.746	0.591	0.696
Error	39.037	16	2.440				

### Small-seeded annuals

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	6.000	1	6.000	2.455	0.192
Error	9.778	4	2.444		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	12.111	2	6.056	1.098	0.379	0.372	0.379
Error	44.111	8	5.514				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.111	2	0.056	0.014	0.987	0.981	0.987
Error	32.778	8	4.097				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	9.778	4	2.444	1.751	0.188	0.223	0.188
Error	22.333	16	1.396				

### Unpalatable plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	14.519	1	14.519	1.709	0.261
Error	33.981	4	8.495		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.037	2	0.019	0.025	0.976	0.973	0.976
Error	5.963	8	0.745				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.704	2	0.352	0.386	0.692	0.631	0.692
Error	7.296	8	0.912				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000

year*season							
*TRMT\$	1.407	4	0.352	0.303	0.872	0.748	0.872
Error	18.593	16	1.162				

### Palatable plants

#### Between Subjects

Source	SS	df	MS	F	P		
TRMT\$	3.130	1	3.130	0.431	0.547		
Error	29.037	4	7.259				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	4.593	2	2.296	0.377	0.698	0.669	0.698
Error	48.741	8	6.093				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	1.037	2	0.519	0.500	0.624	0.549	0.619
Error	8.296	8	1.037				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	6.074	4	1.519	0.429	0.785	0.698	0.785
Error	56.593	16	3.537				

### Palatable forbs

#### Between Subjects

Source	SS	df	MS	F	P		
TRMT\$	4.167	1	4.167	0.393	0.565		
Error	42.444	4	10.611				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.444	2	0.222	0.056	0.946	0.904	0.946
Error	31.778	8	3.972				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.444	2	0.222	0.096	0.909	0.787	0.859
Error	18.444	8	2.306				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	11.111	4	2.778	0.913	0.480	0.453	0.480
Error	48.667	16	3.042				

### Palatable graminoids (summers and falls only)

#### Between Subjects

Source	SS	df	MS	F	P		
TRMT\$	9.000	1	9.000	0.850	0.409		
Error	42.333	4	10.583				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	4.667	2	2.333	0.410	0.677	0.655	0.677
Error	45.500	8	5.687				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	1	0.000	0.000	1.000	.	.
season*TRMT\$	0.444	1	0.444	3.200	0.148	.	.
Error	0.556	4	0.139				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.222	2	0.111	0.696	0.527	0.464	0.505

Error	1.278	8	0.160
-------	-------	---	-------

**Species richness****Between Subjects**

Source	SS	df	MS	F	P
*RABBITACCES\$	1.500	1	1.500	0.192	0.684
Error	31.259	4	7.815		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	81.037	2	40.519	12.432	0.004	0.016	0.004
year*RABBITACCES\$	1.778	2	0.889	0.273	0.768	0.669	0.760
Error	26.074	8	3.259				
Source	SS	df	MS	F	P	G-G	H-F
season	105.037	2	52.519	64.455	0.000	0.000	0.000
season*RABBITACCES\$	17.333	2	8.667	10.636	0.006	0.008	0.006
Error	6.519	8	0.815				
Source	SS	df	MS	F	P	G-G	H-F
year*season	75.741	4	18.935	8.381	0.001	0.009	0.001
year*season*							
RABBITACCES\$	5.889	4	1.472	0.652	0.634	0.555	0.634
Error	36.148	16	2.259				

**Species evenness****Between Subjects**

Source	SS	df	MS	F	P
RABBITACCES\$	0.014	1	0.014	2.098	0.221
Error	0.027	4	0.007		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.033	2	0.017	1.853	0.218	0.244	0.233
year*RABBITACCES\$	0.018	2	0.009	1.011	0.406	0.375	0.392
Error	0.071	8	0.009				
Source	SS	df	MS	F	P	G-G	H-F
season	0.171	2	0.085	14.256	0.002	0.010	0.002
season*RABBITACCES\$	0.055	2	0.027	4.586	0.047	0.079	0.047
Error	0.048	8	0.006				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.091	4	0.023	2.972	0.052	0.123	0.063
year*season*							
RABBITACCES\$	0.014	4	0.004	0.471	0.757	0.612	0.732
Error	0.122	16	0.008				

**Gini diversity****Between Subjects**

Source	SS	df	MS	F	P
RABBITACCES\$	0.014	1	0.014	0.613	0.477
Error	0.090	4	0.022		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.140	2	0.070	2.562	0.138	0.145	0.138
year*RABBITACCES\$	1.018	2	0.009	0.325	0.732	0.716	0.732
Error	0.218	8	0.027				
Source	SS	df	MS	F	P	G-G	H-F
season	0.023	2	0.012	1.989	0.199	0.216	0.199
season*RABBITACCES\$	0.015	2	0.007	1.264	0.333	0.331	0.333
Error	0.047	8	0.006				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.383	4	0.096	26.261	0.000	0.000	0.000
year*season*							
RABBITACCES\$	0.019	4	0.005	1.292	0.315	0.326	0.315
Error	0.058	16	0.004				

## 2. Mid-succession.

## Rabbit-dispersed plants

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	10.667	1	10.667	0.685	0.454		
Error	62.278	4	15.569				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	3.000	2	1.500	2.227	0.170	0.172	0.170
Error	5.389	8	0.674				
Greenhouse-Geisser Epsilon:			0.9820				
Huynh-Feldt Epsilon :			1.0000				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	16.333	2	8.167	3.079	0.102	0.123	0.102
Error	21.222	8	2.653				
Greenhouse-Geisser Epsilon:			0.7698				
Huynh-Feldt Epsilon :			1.0000				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	0.667	4	0.167	0.088	0.985	0.848	0.938
Error	30.444	16	1.903				

## Rabbit-dispersed forbs

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	8.963	1	8.963	2.308	0.203		
Error	15.537	4	3.884				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	6.704	2	3.352	1.135	0.368	0.364	0.368
Error	23.630	8	2.954				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	26.926	2	13.463	5.193	0.036	0.061	0.036
Error	20.741	8	2.593				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	4.407	4	1.102	0.689	0.610	0.507	0.586
Error	25.593	16	1.600				

## Rabbit-dispersed graminoids

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	16.667	1	16.667	1.129	0.348		
Error	59.056	4	14.764				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.778	2	0.389	0.467	0.643	0.548	0.607
Error	6.667	8	0.833				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	1.444	2	0.722	0.413	0.675	0.583	0.655



Error	14.000	8	1.750				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.444	4	0.111	0.132	0.968	0.860	0.968
Error	13.444	16	0.840				

### Annual plants

Between Subjects							
Source	SS	df	MS	F	P	G-G	H-F
TRMT\$	26.741	1	26.741	6.959		<b>0.058</b>	
Error	15.370	4	3.843				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	3.815	2	1.907	0.408	0.678	0.602	0.678
Error	37.407	8	4.676				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	0.926	2	0.463	0.145	0.867	0.763	0.854
Error	25.463	8	3.183				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	9.852	4	2.463	3.304	<b>0.037</b>	0.101	0.040
Error	11.926	16	0.745				

### Small-seeded plants

Between Subjects							
Source	SS	df	MS	F	P	G-G	H-F
TRMT\$	17.796	1	17.796	1.129		0.348	
Error	63.037	4	15.759				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	7.259	2	3.630	2.063	0.189	0.208	0.189
Error	14.074	8	1.759				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	4.593	2	2.296	0.625	0.560	0.490	0.539
Error	29.407	8	3.676				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	1.185	4	0.296	0.235	0.914	0.851	0.914
Error	20.148	16	1.259				

### Small-seeded graminoids

Between Subjects							
Source	SS	df	MS	F	P	G-G	H-F
TRMT\$	25.352	1	25.352	1.052		0.363	
Error	96.370	4	24.093				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	7.704	2	3.852	2.552	0.139	0.147	0.139
Error	12.074	8	1.509				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	0.593	2	0.296	0.278	0.764	0.726	0.764
Error	8.519	8	1.065				
Source	SS	df	MS	F	P	G-G	H-F

YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	1.185	4	0.296	0.831	0.525	0.471	0.525
Error	5.704	16	0.356				

### Small-seeded forbs

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	2.241	1	2.241	0.264	0.634
Error	33.926	4	8.481		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	5.481	2	2.741	0.343	0.719	0.654	0.719
Error	63.852	8	7.981				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	2.370	2	1.185	0.921	0.437	0.406	0.435
Error	10.296	8	1.287				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	3.407	4	0.852	0.379	0.820	0.689	0.820
Error	35.926	16	2.245				

### Unpalatable plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	2.667	1	2.667	0.187	0.688
Error	57.111	4	14.278		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	0.111	2	0.056	0.008	0.992	0.958	0.990
Error	55.111	8	6.889				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	1.444	2	0.722	1.209	0.348	0.340	0.348
Error	4.778	8	0.597				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	3.778	4	0.944	1.511	0.246	0.285	0.272
Error	10.000	16	0.625				

### Palatable plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	13.500	1	13.500	0.593	0.484
Error	91.111	4	22.778		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	0.444	2	0.222	0.082	0.922	0.799	0.867
Error	21.778	8	2.722				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	0.444	2	0.222	0.136	0.875	0.850	0.875
Error	13.111	8	1.639				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							

*TRMT\$	0.444	4	0.111	0.107	0.978	0.848	0.947
Error	16.667	16	1.042				

**Palatable forbs****Between Subjects**

Source	SS	df	MS	F	P
TRMT\$	13.500	1	13.500	0.593	0.484
Error	91.111	4	22.778		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
YEAR	0.000	2	0.000	0.000	1.000	1.000	1.000
YEAR*TRMT\$	0.444	2	0.222	0.082	0.922	0.799	0.867
Error	21.778	8	2.722				
Source	SS	df	MS	F	P	G-G	H-F
SEASON	0.000	2	0.000	0.000	1.000	1.000	1.000
SEASON*TRMT\$	0.444	2	0.222	0.136	0.875	0.850	0.875
Error	13.111	8	1.639				
Source	SS	df	MS	F	P	G-G	H-F
YEAR*SEASON	0.000	4	0.000	0.000	1.000	1.000	1.000
YEAR*SEASON							
*TRMT\$	0.444	4	0.111	0.107	0.978	0.848	0.947
Error	16.667	16	1.042				

**Non-native graminoids****Between Subjects**

Source	SS	df	MS	F	P
TRMT\$	22.685	1	22.685	0.894	0.398
Error	101.481	4	25.370		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	7.259	2	3.630	3.087	0.102	0.128	0.102
Error	9.407	8	1.176				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	1.037	2	0.519	0.544	0.601	0.588	0.601
Error	7.630	8	0.954				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	1.185	4	0.296	0.696	0.606	0.532	0.606
Error	6.815	16	0.426				

**Species richness****Between Subjects**

Source	SS	df	MS	F	P
RABBITACCES\$	8.167	1	8.167	4.240	0.109
Error	7.704	4	1.926		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	83.815	2	41.907	7.242	0.016	0.052	0.032
year*RABBITACCES\$	0.111	2	0.056	0.010	0.990	0.932	0.970
Error	46.296	8	5.787				
Source	SS	df	MS	F	P	G-G	H-F
season	70.037	2	35.019	51.808	0.000	0.000	0.000
season*RABBITACCES\$	10.111	2	5.056	7.479	0.015	0.019	0.015
Error	5.407	8	0.676				
Source	SS	df	MS	F	P	G-G	H-F
year*season	33.074	4	8.269	6.034	0.004	0.027	0.004
year*season*							
RABBITACCES\$	4.111	4	1.028	0.750	0.572	0.499	0.572
Error	21.926	16	1.370				

**Species evenness****Between Subjects**

Source	SS	df	MS	F	P
RABBITACCESS\$	0.180	1	0.180	3.216	0.147
Error	0.224	4	0.056		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.056	2	0.028	1.925	0.208	0.220	0.208
year*RABBITACCESS\$	0.021	2	0.011	0.740	0.507	0.485	0.507
Error	0.116	8	0.015				
Source	SS	df	MS	F	P	G-G	H-F
season	0.084	2	0.042	6.506	0.021	0.057	0.034
season*RABBITACCESS\$	0.000	2	0.000	0.029	0.971	0.889	0.945
Error	0.052	8	0.006				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.022	4	0.005	0.390	0.812	0.631	0.738
year*season*RABBITACCESS\$	0.020	4	0.005	0.352	0.839	0.653	0.764
Error	0.223	16	0.014				

**Gini diversity****Between Subjects**

Source	SS	df	MS	F	P
RABBITACCESS\$	0.091	1	0.091	1.044	0.365
Error	0.348	4	0.087		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.774	2	0.387	7.734	0.014	0.045	0.025
year*RABBITACCESS\$	0.003	2	0.002	0.032	0.968	0.882	0.939
Error	0.400	8	0.050				
Source	SS	df	MS	F	P	G-G	H-F
season	0.087	2	0.044	6.795	0.019	0.026	0.019
season*RABBITACCESS\$	0.009	2	0.004	0.696	0.527	0.510	0.527
Error	0.052	8	0.006				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.110	4	0.027	3.040	0.048	0.097	0.048
year*season*RABBITACCESS\$	0.026	4	0.007	0.735	0.581	0.518	0.581
Error	0.144	16	0.009				

**3. Late succession.****Rabbit-dispersed plants (2002, 2003 only)****Between Subjects**

Source	SS	df	MS	F	P
TRMT\$	0.000	1	0.000	2.236	0.209
Error	0.000	4	0.000		

**Within Subjects**

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	1	0.000	0.235	0.653	.	.
year*TRMT\$	0.000	1	0.000	0.174	0.698	.	.
Error	0.000	4	0.000				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	5.388	0.033	0.055	0.033
season*TRMT\$	0.000	2	0.000	2.117	0.183	0.204	0.183
Error	0.000	8	0.000				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.276	0.766	0.637	0.704
year*season*TRMT\$	0.000	2	0.000	0.351	0.714	0.595	0.656
Error	0.000	8	0.000				

## Rabbit-dispersed forbs (2002 only)

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.000	1	0.000	0.003	0.957		
Error	0.000	4	0.000				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	1.447	0.291	0.294	0.291
season*TRMT\$	0.000	2	0.000	0.527	0.610	0.581	0.610
Error	0.000	8	0.000				

## Rabbit-dispersed graminoids (springs only)

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.000	1	0.000	2.236	0.209		
Error	0.000	4	0.000				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	1	0.000	0.235	0.653	.	.
year*TRMT\$	0.000	1	0.000	0.174	0.698	.	.
Error	0.000	4	0.000				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	5.388	0.033	0.055	0.033
season*TRMT\$	0.000	2	0.000	2.117	0.183	0.204	0.183
Error	0.000	8	0.000				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.276	0.766	0.637	0.704
year*season*TRMT\$	0.000	2	0.000	0.351	0.714	0.595	0.656
Error	0.000	8	0.000				

## Annual plants

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	18.963	1	18.963	0.636	0.470		
Error	119.259	4	29.815				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.481	2	0.241	0.323	0.733	0.622	0.696
Error	5.963	8	0.745				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.481	2	0.241	0.584	0.580	0.578	0.580
Error	3.296	8	0.412				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	1.407	4	0.352	0.788	0.550	0.465	0.525
Error	7.148	16	0.447				

## Small-seeded plants

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	4.167	1	4.167	0.178	0.695		
Error	93.556	4	23.389				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	3.111	2	1.556	0.747	0.504	0.468	0.504

Error	16.667	8	2.083				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	1.333	2	0.667	0.387	0.691	0.618	0.691
Error	13.778	8	1.722				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	10.222	4	2.556	2.788	0.062	0.119	0.062
Error	14.667	16	0.917				

### Small-seeded graminoids

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	53.778	1	53.778	5.939	0.071
Error	36.222	4	9.056		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	1	0.000	0.000	1.000	.	.
year*TRMT\$	2.778	1	2.778	2.273	0.206	.	.
Error	4.889	4	1.222				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.222	2	0.111	0.235	0.796	0.696	0.790
Error	3.778	8	0.472				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.222	2	0.111	0.286	0.759	0.635	0.704
Error	3.111	8	0.389				

### Small-seeded forbs

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	104.167	1	104.167	11.029	0.029
Error	37.778	4	9.444		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	1.333	2	0.667	1.263	0.334	0.333	0.334
Error	4.222	8	0.528				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.444	2	0.222	0.400	0.683	0.584	0.654
Error	4.444	8	0.556				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.889	4	0.222	0.842	0.519	0.463	0.519
Error	4.222	16	0.264				

### Non-native forbs

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	68.907	1	68.907	18.063	0.013
Error	15.259	4	3.815		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.148	2	0.074	0.014	0.986	0.930	0.974
Error	42.519	8	5.315				
Source	SS	df	MS	F	P	G-G	H-F

season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	1.037	2	0.519	0.378	0.697	0.618	0.697
Error	10.963	8	1.370				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	4.741	4	1.185	1.362	0.291	0.311	0.292
Error	13.926	16	0.870				

### Unpalatable plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	18.963	1	18.963	0.638	0.469
Error	118.815	4	29.704		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.481	2	0.241	0.249	0.786	0.684	0.774
Error	7.741	8	0.968				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.481	2	0.241	0.800	0.482	0.472	0.482
Error	2.407	8	0.301				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	1.407	4	0.352	0.840	0.520	0.439	0.483
Error	6.704	16	0.419				

### Palatable plants

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.667	1	0.667	0.036	0.859
Error	74.778	4	18.694		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	3.000	2	1.500	1.831	0.222	0.239	0.222
Error	6.556	8	0.819				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.778	2	0.389	0.118	0.890	0.800	0.890
Error	26.278	8	3.285				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*TRMT\$	0.889	4	0.222	0.169	0.951	0.874	0.951
Error	21.056	16	1.316				

### Palatable graminoids (only springs)

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	10.889	1	10.889	4.455	0.102
Error	9.778	4	2.444		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	3.444	2	1.722	0.867	0.456	0.422	0.456
Error	15.889	8	1.986				

### Palatable forbs

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
TRMT\$	0.019	1	0.019	0.001	0.978		
Error	85.037	4	21.259				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	1.037	2	0.519	0.586	0.579	0.497	0.543
Error	7.074	8	0.884				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.148	2	0.074	0.036	0.965	0.888	0.951
Error	16.463	8	2.058				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	2.963	4	0.741	1.008	0.432	0.400	0.430
Error	11.759	16	0.735				

### Woody seedlings

Between Subjects							
Source	SS	df	MS	F	P	G-G	H-F
TRMT\$	0.167	1	0.167	0.008	0.934		
Error	84.556	4	21.139				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*TRMT\$	0.444	2	0.222	0.119	0.890	0.799	0.890
Error	15.000	8	1.875				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*TRMT\$	0.444	2	0.222	0.115	0.893	0.761	0.830
Error	15.500	8	1.938				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*TRMT\$	1.778	4	0.444	0.564	0.692	0.535	0.610
Error	12.611	16	0.788				

### Species richness

Between Subjects							
Source	SS	df	MS	F	P	G-G	H-F
RABBITACCES\$	2.241	1	2.241	0.095	0.773		
Error	93.926	4	23.481				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	11.444	2	5.722	2.664	0.130	0.158	0.130
year*RABBITACCES\$	3.370	2	1.685	0.784	0.489	0.455	0.489
Error	17.185	8	2.148				
Source	SS	df	MS	F	P	G-G	H-F
season	16.444	2	8.222	8.621	0.010	0.035	0.016
season*RABBITACCES\$	0.593	2	0.296	0.311	0.741	0.632	0.709
Error	7.630	8	0.954				
Source	SS	df	MS	F	P	G-G	H-F
year*season	2.111	4	0.528	0.708	0.598	0.487	0.552
year*season*RABBITACCES\$	0.630	4	0.157	0.211	0.928	0.750	0.866
Error	11.926	16	0.745				

### Species evenness

Between Subjects					
Source	SS	df	MS	F	P



RABBITACCESS\$	0.354	1	0.354	2.605	0.182		
Error	0.544	4	0.136				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.003	2	0.002	0.114	0.894	0.835	0.894
year*RABBITACCESS\$	0.011	2	0.005	0.407	0.678	0.623	0.678
Error	0.105	8	0.013				
Source	SS	df	MS	F	P	G-G	H-F
season	0.016	2	0.008	2.046	0.192	0.211	0.192
season*RABBITACCESS\$	0.012	2	0.006	1.608	0.259	0.269	0.259
Error	0.031	8	0.004				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.065	4	0.016	3.065	0.047	0.139	0.100
year*season*							
RABBITACCESS\$	0.024	4	0.006	1.114	0.384	0.360	0.375
Error	0.085	16	0.005				

### Gini diversity

Between Subjects							
Source	SS	df	MS	F	P		
RABBITACCESS\$	0.150	1	0.150	4.803	0.094		
Error	0.125	4	0.031				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.012	2	0.006	0.916	0.438	0.433	0.438
year*RABBITACCESS\$	0.011	2	0.006	0.843	0.465	0.458	0.465
Error	0.053	8	0.007				
Source	SS	df	MS	F	P	G-G	H-F
season	0.007	2	0.003	0.576	0.584	0.579	0.584
season*RABBITACCESS\$	0.009	2	0.004	0.757	0.500	0.496	0.500
Error	0.046	8	0.006				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.045	4	0.011	5.092	0.008	0.032	0.008
year*season*							
RABBITACCESS\$	0.012	4	0.003	1.343	0.297	0.313	0.297
Error	0.035	16	0.002				

## APPENDIX B.

Statistical values of Mann-Whitney analyses of individual plant species' response to rabbit access, in the season of the plants' highest abundance, in 1) early succession, 2) mid-succession, and 3) late succession.  $n_1=3$ ,  $n_2=6$  for all.

### 1. Early succession

2002		U-statistic	P-value
<i>Oxalis corniculata</i>	summer	6.0	0.396
<i>Medicago sativa</i>	summer	9.0	1.000
<i>Chamaesyce maculata</i>	summer	4.5	0.225
<i>Echinochloa crus-galli</i>	summer	12.0	0.418
<i>Mollugo verticillata</i>	summer	8.0	0.724
<i>Abutilon theophrasti</i>	summer	13.5	0.167
<i>Setaria italica</i>	summer	11.0	0.606
<i>Polygonum persicaria</i>	summer	10.0	0.796
<i>Sida spinosa</i>	summer	4.0	0.195
<i>Amaranthus retroflexus</i>	fall	11.0	0.606
<i>Digitaria sanguinalis</i>	fall	11.0	0.606
<i>Panicum capillare</i>	fall	4.0	0.189
2003			
<i>Medicago sativa</i>	spring	10.0	0.796
<i>Polygonum persicaria</i>	spring	9.0	1.000
<i>Oxalis corniculata</i>	spring	7.0	0.599
<i>Capsella bursa-pastoris</i>	spring	9.0	1.000
<i>Conyza canadensis</i>	summer	11.0	0.606
<i>Sida spinosa</i>	fall	4.0	0.181
<i>Setaria italica</i>	fall	5.0	0.302
2004			
<i>Medicago sativa</i>	spring	9.0	1.000
<i>Geum canadense</i>	spring	9.0	1.000
<i>Polygonum persicaria</i>	spring	7.0	0.606
<i>Oxalis corniculata</i>	spring	13.0	0.302
<i>Cirsium arvense</i>	spring	5.0	0.294
<i>Abutilon theophrasti</i>	summer	17.5	0.026
<i>Conyza canadensis</i>	summer	10.0	0.786
<i>Sida spinosa</i>	summer	10.5	0.696
<i>Digitaria sanguinalis</i>	fall	8.0	0.796
<i>Panicum capillare</i>	fall	6.0	0.396
<i>Solidago canadensis</i>	fall	3.0	0.118
<i>Setaria italica</i>	fall	12.0	0.439

### 2. Mid-succession

2002		U-statistic	P-value
<i>Geum canadense</i>	spring	13	0.281
<i>Dactylis glomerata</i>	spring	9.5	0.897
<i>Galium asprellum</i>	spring	7.5	0.696

<i>Festuca elatior</i>	spring	13	0.302
<i>Elymus canadensis</i>	spring	12	0.396
<i>Taraxacum officinale</i>	spring	12	0.439
<i>Rumex crispus</i>	spring	11.5	0.502
<i>Bromus japonicus</i>	summer	6.5	0.5
<i>Cirsium arvense</i>	summer	10	0.759
<i>Medicago sativa</i>	summer	14	0.197
<i>Aster ericoides</i>	fall	12	0.439
<i>Solidago canadensis</i>	fall	3	0.121

## 2003

<i>Geum canadense</i>	spring	8	0.777
<i>Taraxacum officinale</i>	spring	12	0.439
<i>Galium asprellum</i>	spring	4	0.197
<i>Dactylis glomerata</i>	spring	12	0.439
<i>Medicago sativa</i>	spring	16	0.071
<i>Cirsium arvense</i>	spring	13.5	0.243
<i>Festuca elatior</i>	spring	8	0.796
<i>Rumex crispus</i>	spring	7	0.599
<i>Thlaspi arvense</i>	spring	5	0.3
<i>Bromus japonicus</i>	summer	6	0.396
<i>Solidago canadensis</i>	summer	3	0.121
<i>Poa pratensis</i>	summer	6.5	0.5
<i>Aster ericoides</i>	fall	12	0.439

## 2004

<i>Festuca elatior</i>	spring	13	0.302
<i>Galium asprellum</i>	spring	7.5	0.686
<i>Rumex crispus</i>	spring	11.5	0.51
<i>Poa pratensis</i>	spring	7	0.572
<i>Medicago sativa</i>	spring	9	1
<i>Thlaspi arvense</i>	spring	1	0.036
<i>Taraxacum officinale</i>	spring	10	0.796
<i>Dactylis glomerata</i>	spring	13	0.302
<i>Solidago canadensis</i>	summer	5	0.302
<i>Aster ericoides</i>	fall	13	0.302
<i>Cirsium arvense</i>	fall	4	0.195

## 3. Late succession

		U-statistic	P-value
2002			
<i>Galium asprellum</i>	spring	12	0.423
<i>Festuca elatior</i>	spring	11	0.606
<i>Barbarea vulgaris</i>	spring	9	1
<i>Pastinaca sativa</i>	spring	9	1
<i>Poa pratensis</i>	spring	4	0.195
<i>Cirsium arvense</i>	summer	6	0.439
<i>Bromus inermis</i>	fall	12	0.439
<i>Solanum carolinense</i>	fall	8	0.777
<i>Solidago canadensis</i>	fall	7	0.606

## 2003

<i>Bromus inermis</i>	spring	13	0.302
<i>Carex laevivaginata</i>	spring	14	0.181
<i>Poa pratensis</i>	spring	6	0.439
<i>Pastinaca sativa</i>	spring	8	0.796
<i>Barbarea vulgaris</i>	spring	11	0.572
<i>Solidago canadensis</i>	summer	3	0.121
<i>Cirsium arvense</i>	summer	7.5	0.697
<i>Festuca elatior</i>	fall	11	0.606

## 2004

<i>Barbarea vulgaris</i>	spring	10	0.776
<i>Poa pratensis</i>	spring	8	0.796
<i>Pastinaca sativa</i>	spring	6	0.439
<i>Carex laevivaginata</i>	spring	15	0.09
<i>Bromus inermis</i>	summer	11	0.606
<i>Cirsium arvense</i>	summer	9	1
<i>Solidago canadensis</i>	summer	3	0.121
<i>Festuca elatior</i>	fall	18	0.02

## APPENDIX C.

Statistical tables for repeated measures ANOVA testing hypotheses regarding rodent access to plots in 1) early succession, 2) mid-succession, and 3) late succession.

## 1. Early succession

## Palatable plants

## Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	44.056	2	22.028	0.612	0.573
Error	216.111	6	36.019		

## Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	22.556	4	5.639	0.777	0.561	0.525	0.561
Error	87.111	12	7.259				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	12.222	4	3.056	0.864	0.513	0.502	0.513
Error	42.444	12	3.537				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	26.333	8	3.292	0.912	0.524	0.476	0.505
Error	86.667	24	3.611				

## Palatable forbs

## Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	40.574	2	20.287	0.563	0.597
Error	216.037	6	36.006		

## Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	22.481	4	5.620	0.796	0.550	0.509	0.544
Error	84.741	12	7.062				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	12.593	4	3.148	0.866	0.512	0.506	0.512
Error	43.630	12	3.636				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	27.519	8	3.440	0.918	0.519	0.475	0.503
Error	89.926	24	3.747				

(palatable graminoids too few for analysis)

## Unpalatable plants

## Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.889	2	0.444	0.042	0.959
Error	63.333	6	10.556		

## Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
--------	----	----	----	---	---	-----	-----

year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	12.222	4	3.056	0.392	0.811	0.794	0.811
Error	93.556	12	7.796				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	20.222	4	5.056	0.597	0.672	0.620	0.672
Error	101.556	12	8.463				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	19.333	8	2.417	0.253	0.975	0.893	0.968
Error	228.889	24	9.537				

### Plants with palatable seeds

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.037	2	0.018	0.258	0.781
Error	0.426	6	0.071		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.632	2	0.316	9.201	0.004	0.013	0.004
year*ACCESS\$	0.144	4	0.036	1.047	0.423	0.415	0.423
Error	0.412	12	0.034				
Source	SS	df	MS	F	P	G-G	H-F
Season	0.125	2	0.062	1.630	0.236	0.249	0.245
season*ACCESS\$	0.161	4	0.040	1.052	0.421	0.406	0.415
Error	0.459	12	0.038				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.768	4	0.192	4.872	0.005	0.040	0.014
year*season* ACCESS\$	0.059	8	0.007	0.186	0.991	0.913	0.973
Error	0.945	24	0.039				

### Large-seeded plants (only 2004)

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	31.056	2	15.528	3.838	<b>0.084</b>
Error	24.278	6	4.046		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	24.778	4	6.194	1.962	0.165	0.180	0.165
Error	37.889	12	3.157				

### Annual plants

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	31.352	2	15.676	1.491	0.298
Error	63.093	6	10.515		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	54.926	4	13.731	1.798	0.194	0.196	0.194
Error	91.630	12	7.636				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	8.593	4	2.148	0.561	0.696	0.604	0.654
Error	45.963	12	3.830				
Source	SS	df	MS	F	P	G-G	H-F

year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	48.963	8	6.120	0.957	0.491	0.465	0.490
Error	153.481	24	6.395				

### Woody seedlings

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	2.528	2	1.264	0.115	0.893
Error	66.056	6	11.009		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	1	0.000	0.000	1.000	.	.
year*ACCESS\$	18.361	2	9.181	4.699	<b>0.059</b>	.	.
Error	11.722	6	1.954				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	22.556	4	5.639	1.228	0.350	0.351	0.350
Error	55.111	12	4.593				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	6.222	4	1.556	0.218	0.923	0.858	0.923
Error	85.444	12	7.120				

### Species richness

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	1.877	2	0.938	0.109	0.899
Error	51.704	6	8.617		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	50.469	2	25.235	4.913	0.028	0.044	0.028
year*ACCESS\$	10.568	4	2.642	0.514	0.727	0.680	0.727
Error	61.630	12	5.136				
Source	SS	df	MS	F	P	G-G	H-F
season	131.877	2	65.938	33.486	0.000	0.000	0.000
season							
*ACCESS\$	0.494	4	0.123	0.063	0.992	0.989	0.992
Error	23.630	12	1.969				
Source	SS	df	MS	F	P	G-G	H-F
year*season	119.901	4	29.975	12.050	0.000	0.001	0.000
year*season							
*ACCESS\$	23.728	8	2.966	1.192	0.344	0.364	0.345
Error	59.704	24	2.488				

### Species evenness

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.000	2	0.000	0.005	0.995
Error	0.139	6	0.023		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.072	2	0.036	3.176	0.078	0.080	0.078
year*ACCESS\$	0.027	4	0.007	0.605	0.667	0.662	0.667
Error	0.135	12	0.011				
Source	SS	df	MS	F	P	G-G	H-F
season	0.179	2	0.090	7.268	0.009	0.011	0.009
season*ACCESS\$	0.026	4	0.006	0.524	0.720	0.704	0.720
Error	0.148	12	0.012				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.024	4	0.006	0.522	0.720	0.573	0.666
year*season							
*ACCESS\$	0.092	8	0.012	0.994	0.465	0.441	0.457
Error	0.279	24	0.012				

### Gini diversity

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.024	2	0.012	0.348	0.720
Error	0.203	6	0.034		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.195	2	0.097	3.635	0.058	0.094	0.064
year*ACCESS\$	0.121	4	0.030	1.128	0.389	0.386	0.389
Error	0.321	12	0.027				

Source	SS	df	MS	F	P	G-G	H-F
season	0.009	2	0.005	0.376	0.694	0.681	0.694
season							
*ACCESS\$	0.013	4	0.003	0.260	0.898	0.888	0.898
Error	0.145	12	0.012				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.345	4	0.086	9.613	0.000	0.004	0.000
year*season							
*ACCESS\$	0.077	8	0.010	1.073	0.414	0.411	0.414
Error	0.215	24	0.009				

## 2. Mid-succession

### Palatable plants

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	57.556	2	28.778	2.391	0.172
Error	72.222	6	12.037		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	23.778	4	5.944	0.599	0.671	0.600	0.654
Error	119.111	12	9.926				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	80.444	4	20.111	2.311	0.117	0.175	0.143
Error	104.444	12	8.704				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	6.889	8	0.861	0.274	0.969	0.868	0.950
Error	75.556	24	3.148				

### Palatable forbs

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	350.519	2	175.259	14.791	0.005
Error	71.093	6	11.849		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	3.259	4	0.815	0.280	0.886	0.777	0.843
Error	34.963	12	2.914				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000



season*ACCESS\$	1.259	4	0.315	0.320	0.859	0.788	0.859
Error	11.796	12	0.983				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	7.630	8	0.954	0.428	0.893	0.824	0.893
Error	53.481	24	2.228				

### Palatable graminoids

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	40.963	2	20.481	3.790	<b>0.086</b>		
Error	32.426	6	5.404				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	27.259	4	6.815	0.552	0.702	0.627	0.687
Error	148.185	12	12.349				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	40.815	4	10.204	0.957	0.466	0.440	0.457
Error	127.963	12	10.664				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	32.963	8	4.120	1.112	0.390	0.395	0.390
Error	88.926	24	3.705				

### Unpalatable plants

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	23.722	2	11.861	0.430	0.669		
Error	165.500	6	27.583				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	44.556	4	11.139	5.065	<b>0.013</b>	0.018	0.013
Error	26.389	12	2.199				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	28.111	4	7.028	1.515	0.259	0.262	0.259
Error	55.667	12	4.639				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	26.944	8	3.368	0.516	0.832	0.756	0.832
Error	156.611	24	6.525				

### Annual plants

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	17.241	2	8.620	0.497	0.631		
Error	103.981	6	17.330				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	8.037	4	2.009	0.304	0.870	0.844	0.870
Error	79.241	12	6.603				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	32.037	4	8.009	1.979	0.162	0.181	0.162

Error	48.574	12	4.048				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	19.852	8	2.481	0.390	0.915	0.858	0.915
Error	152.537	24	6.356				

### Large-seeded plants

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	30.500	2	15.250	0.930	0.445		
Error	98.389	6	16.398				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	10.000	4	2.500	1.149	0.380	0.381	0.380
Error	26.111	12	2.176				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	2.500	4	0.625	0.029	0.998	0.974	0.992
Error	260.944	12	21.745				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	13.667	8	1.708	1.054	0.426	0.423	0.426
Error	38.889	24	1.620				

### Plants with palatable seeds

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	0.242	2	0.121	21.407	0.002		
Error	0.034	6	0.006				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.327	2	0.163	97.572	0.000	0.000	0.000
year*ACCESS\$	0.053	4	0.013	7.888	0.002	0.011	0.002
Error	0.020	12	0.002				
Source	SS	df	MS	F	P	G-G	H-F
season	0.001	2	0.001	0.293	0.751	0.735	0.751
season* ACCESS\$	0.005	4	0.001	0.534	0.713	0.701	0.713
Error	0.026	12	0.002				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.061	4	0.015	9.718	0.000	0.011	0.003
year*season*ACCESS\$	0.037	8	0.005	2.920	0.020	0.105	0.063
Error	0.038	24	0.002				

### Species richness

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	4.667	2	2.333	0.243	0.791		
Error	57.556	6	9.593				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	106.889	2	53.444	8.538	0.005	0.012	0.005
year*ACCESS\$	9.778	4	2.444	0.391	0.812	0.760	0.812
Error	75.111	12	6.259				
Source	SS	df	MS	F	P	G-G	H-F
season	20.519	2	10.259	6.368	0.013	0.025	0.013
season*ACCESS\$	11.926	4	2.981	1.851	0.184	0.209	0.184
Error	19.333	12	1.611				
Source	SS	df	MS	F	P	G-G	H-F

year*season	54.815	4	13.704	7.708	0.000	0.002	0.000
year*season							
*ACCESS\$	32.741	8	4.093	2.302	<b>0.055</b>	0.085	0.055
Error	42.667	24	1.778				

### Species evenness

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	0.931	2	0.465	87.856	<b>&lt;0.001</b>		
Error	0.032	6	0.005				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.163	2	0.081	9.895	0.003	0.004	0.003
year*ACCESS\$	0.054	4	0.013	1.630	0.230	0.234	0.230
Error	0.099	12	0.008				
Source	SS	df	MS	F	P	G-G	H-F
season	0.066	2	0.033	4.427	0.036	0.060	0.036
season*ACCESS\$	0.030	4	0.008	1.011	0.440	0.429	0.440
Error	0.089	12	0.007				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.047	4	0.012	1.673	0.189	0.227	0.189
year*season							
*ACCESS\$	0.042	8	0.005	0.750	0.648	0.580	0.648
Error	0.170	24	0.007				

### Gini diversity

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	0.932	2	0.466	14.474	<b>0.005</b>		
Error	0.193	6	0.032				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.923	2	0.461	33.080	0.000	0.001	0.000
year*ACCESS\$	0.308	4	0.077	5.513	<b>0.009</b>	0.040	0.019
Error	0.167	12	0.014				
Source	SS	df	MS	F	P	G-G	H-F
season	0.138	2	0.069	18.374	0.000	0.004	0.001
season*ACCESS\$	0.024	4	0.006	1.628	0.231	0.268	0.247
Error	0.045	12	0.004				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.119	4	0.030	4.487	0.008	0.028	0.008
year*season							
*ACCESS\$	0.021	8	0.003	0.390	0.915	0.834	0.915
Error	0.159	24	0.007				

## 3. Late succession

### Palatable plants

#### Between Subjects

Source	SS	df	MS	F	P	G-G	H-F
ACCESS\$	338.074	2	169.037	8.749	0.017		
Error	115.926	6	19.321				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	1.704	4	0.426	0.236	0.912	0.883	0.912
Error	21.630	12	1.802				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	2.370	4	0.593	0.375	0.822	0.767	0.822
Error	18.963	12	1.580				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*ACCESS\$	11.852	8	1.481	1.206	0.337	0.361	0.350
Error	29.481	24	1.228				

### Palatable forbs

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	18.375	2	9.188	2.141	0.199
Error	25.750	6	4.292		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	1	0.000	0.000	1.000	.	.
year*ACCESS\$	38.625	2	19.312	4.030	<b>0.078</b>	.	.
Error	28.750	6	4.792				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	1	0.000	0.000	1.000	.	.
season*ACCESS\$	2.625	2	1.312	0.432	0.668	.	.
Error	18.250	6	3.042				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	1	0.000	0.000	1.000	.	.
year*season*ACCESS\$	0.375	2	0.187	0.346	0.721	.	.
Error	3.250	6	0.542				

### Palatable graminoids

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	338.296	2	169.148	9.140	<b>0.015</b>
Error	111.037	6	18.506		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	1.259	4	0.315	0.161	0.954	0.934	0.954
Error	23.407	12	1.951				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	3.259	4	0.815	0.541	0.709	0.668	0.709
Error	18.074	12	1.506				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season*ACCESS\$	14.519	8	1.815	1.445	0.229	0.295	0.268
Error	30.148	24	1.256				

### Unpalatable plants

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	329.407	2	164.704	7.606	0.023
Error	129.926	6	21.654		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	1.259	4	0.315	0.195	0.936	0.899	0.936
Error	19.407	12	1.617				

Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	2.148	4	0.537	0.314	0.863	0.810	0.863
Error	20.519	12	1.710				

Source	SS	df	MS	F	P	G-G	H-F
--------	----	----	----	---	---	-----	-----

year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	11.185	8	1.398	1.283	0.298	0.334	0.309
Error	26.148	24	1.090				

### Plants with palatable seeds

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.200	2	0.100	5.643	0.042
Error	0.106	6	0.018		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.022	2	0.011	4.841	0.029	0.043	0.029
year*ACCESS\$	0.005	4	0.001	0.534	0.713	0.675	0.713
Error	0.027	12	0.002				
Source	SS	df	MS	F	P	G-G	H-F
season	0.047	2	0.024	13.464	0.001	0.007	0.001
season*ACCESS\$	0.004	4	0.001	0.524	0.720	0.641	0.703
Error	0.021	12	0.002				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.006	4	0.002	1.079	0.389	0.378	0.389
year*season							
*ACCESS\$	0.007	8	0.001	0.631	0.744	0.679	0.744
Error	0.034	24	0.001				

### Woody plants

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	29.685	2	14.843	0.474	0.644
Error	187.870	6	31.312		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	0.870	4	0.218	0.031	0.998	0.975	0.993
Error	84.074	12	7.006				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season*ACCESS\$	2.426	4	0.606	0.112	0.976	0.928	0.974
Error	65.185	12	5.432				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	22.685	8	2.836	1.540	0.196	0.260	0.213
Error	44.204	24	1.842				

### Large-seeded plants (summers and falls only)

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	78.361	2	39.181	4.175	0.073
Error	56.306	6	9.384		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	5.139	4	1.285	0.391	0.811	0.761	0.811
Error	39.444	12	3.287				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	1	0.000	0.000	1.000	.	.
season*ACCESS\$	2.528	2	1.264	0.913	0.451	.	.
Error	8.306	6	1.384				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	2	0.000	0.000	1.000	1.000	1.000

year*season							
*ACCESS\$	2.972	4	0.743	0.170	0.950	0.879	0.940
Error	52.444	12	4.370				

### Annual plants

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	51.185	2	25.593	0.367	0.707		
Error	417.926	6	69.654				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.000	1.000	1.000	1.000
year*ACCESS\$	16.593	4	4.148	2.233	0.126	0.150	0.126
Error	22.296	12	1.858				
Source	SS	df	MS	F	P	G-G	H-F
season	0.000	2	0.000	0.000	1.000	1.000	1.000
season							
*ACCESS\$	1.037	4	0.259	0.339	0.847	0.796	0.847
Error	9.185	12	0.765				
Source	SS	df	MS	F	P	G-G	H-F
year*season	0.000	4	0.000	0.000	1.000	1.000	1.000
year*season							
*ACCESS\$	3.852	8	0.481	0.683	0.702	0.649	0.702
Error	16.926	24	0.705				

### Species richness

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	1.556	2	0.778	0.042	0.959		
Error	111.333	6	18.556				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	12.963	2	6.481	6.481	0.012	0.024	0.012
year*ACCESS\$	16.148	4	4.037	4.037	0.027	0.046	0.027
Error	12.000	12	1.000				
Source	SS	df	MS	F	P	G-G	H-F
season	16.889	2	8.444	3.257	0.074	0.102	0.074
season							
*ACCESS\$	7.778	4	1.944	0.750	0.577	0.540	0.577
Error	31.111	12	2.593				
Source	SS	df	MS	F	P	G-G	H-F
year*season	8.593	4	2.148	1.568	0.215	0.255	0.239
year*season							
*ACCESS\$	14.741	8	1.843	1.345	0.270	0.320	0.298
Error	32.889	24	1.370				

### Species evenness

#### Between Subjects

Source	SS	df	MS	F	P		
ACCESS\$	0.482	2	0.241	2.205	0.191		
Error	0.656	6	0.109				

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.023	2	0.011	1.085	0.369	0.351	0.369
year*ACCESS\$	0.068	4	0.017	1.615	0.234	0.262	0.234
Error	0.126	12	0.011				
Source	SS	df	MS	F	P	G-G	H-F
season	0.038	2	0.019	2.088	0.167	0.183	0.167
season							
*ACCESS\$	0.032	4	0.008	0.876	0.506	0.489	0.506
Error	0.108	12	0.009				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.103	4	0.026	3.966	0.013	0.066	0.032
year*season							
*ACCESS\$	0.060	8	0.008	1.157	0.364	0.379	0.374
Error	0.156	24	0.007				

### Gini diversity

#### Between Subjects

Source	SS	df	MS	F	P
ACCESS\$	0.221	2	0.110	1.671	0.265
Error	0.396	6	0.066		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
year	0.063	2	0.032	2.132	0.161	0.190	0.171
year*ACCESS\$	0.027	4	0.007	0.447	0.772	0.680	0.745
Error	0.179	12	0.015				

Source	SS	df	MS	F	P	G-G	H-F
season	0.024	2	0.012	5.079	0.025	0.040	0.025
season							
*ACCESS\$	0.039	4	0.010	4.109	<u>0.025</u>	0.043	0.025
Error	0.028	12	0.002				

Source	SS	df	MS	F	P	G-G	H-F
year*season	0.075	4	0.019	12.401	0.000	0.001	0.000
year*season							
*ACCESS\$	0.010	8	0.001	0.819	0.594	0.549	0.594
Error	0.036	24	0.002				

## APPENDIX D.

Statistical values of Kruskal-Wallis analyses of individual plant species' response to rodent access in 1) early succession, 2) mid-succession, and 3) late succession.

## 1) Early succession

2002	H <sub>3,3,3</sub>	P-value
<i>Abutilon theophrasti</i>	2.000	0.368
<i>Amaranthus retroflexus</i>	1.277	0.528
<i>Aster ericoides</i>	0.000	1.000
<i>Chamaesyce maculata</i>	0.368	0.832
<i>Cirsium arvense</i>	2.000	0.368
<i>Conyza canadensis</i>	1.156	0.561
<i>Digitaria sanguinalis</i>	0.089	0.957
<i>Medicago sativa</i>	2.222	0.329
<i>Mollugo verticillata</i>	1.387	0.500
<i>Oxalis corniculata</i>	2.987	0.225
<i>Panicum capillare</i>	1.422	0.491
<i>Physalis subglabrata</i>	0.509	0.775
<i>Polygonum persicaria</i>	0.622	0.733
<i>Setaria italica</i>	0.267	0.875
<i>Sida spinosa</i>	2.851	0.240
<i>Solanum ptychanthum</i>	0.107	0.948
<i>Solidago canadensis</i>	0.000	1.000
<i>Taraxacum officinale</i>	2.000	0.368

2003	H <sub>3,3,3</sub>	P-value
<i>Abutilon theophrasti</i>	0.000	1.000
<i>Amaranthus retroflexus</i>	1.000	0.368
<i>Aster ericoides</i>	2.715	0.257
<i>Chamaesyce maculata</i>	2.000	0.368
<i>Cirsium arvense</i>	2.102	0.350
<i>Conyza canadensis</i>	1.689	0.430
<i>Digitaria sanguinalis</i>	0.125	0.939
<i>Medicago sativa</i>	1.156	0.561
<i>Mollugo verticillata</i>	0.000	1.000
<i>Oxalis corniculata</i>	1.367	0.505
<i>Panicum capillare</i>	0.000	1.000
<i>Physalis subglabrata</i>	0.747	0.688
<i>Polygonum persicaria</i>	1.098	0.578
<i>Setaria italica</i>	1.689	0.430
<i>Sida spinosa</i>	2.952	0.229
<i>Solanum ptychanthum</i>	1.167	0.558
<i>Solidago canadensis</i>	1.167	0.558
<i>Taraxacum officinale</i>	1.167	0.558

2004	H <sub>3,3,3</sub>	P-value
<i>Abutilon theophrasti</i>	4.914	0.086
<i>Amaranthus retroflexus</i>	2.000	0.368
<i>Aster ericoides</i>	3.006	0.223



<i>Chamaesyce maculata</i>	7.714	0.021
<i>Cirsium arvense</i>	0.964	0.618
<i>Conyza canadensis</i>	1.693	0.429
<i>Digitaria sanguinalis</i>	1.689	0.430
<i>Medicago sativa</i>	0.356	0.837
<i>Mollugo verticillata</i>	0.000	1.000
<i>Oxalis corniculata</i>	2.222	0.329
<i>Panicum capillare</i>	3.310	0.191
<i>Physalis subglabrata</i>	0.125	0.939
<i>Polygonum persicaria</i>	0.695	0.707
<i>Setaria italica</i>	1.067	0.587
<i>Sida spinosa</i>	3.988	0.136
<i>Solanum ptychanthum</i>	0.108	0.948
<i>Solidago canadensis</i>	1.098	0.578
<i>Taraxacum officinale</i>	0.022	0.989

## 2) Mid-succession

2002	$H_{3,3,3}$	P-value
<i>Ambrosia trifida</i>	0.747	0.688
<i>Aster ericoides</i>	0.157	0.925
<i>Bromus japonicus</i>	1.785	0.410
<i>Cirsium arvense</i>	6.788	0.034
<i>Dactylis glomerata</i>	0.356	0.837
<i>Festuca elatior</i>	0.089	0.957
<i>Galium asprellum</i>	2.622	0.270
<i>Geum canadense</i>	4.252	0.119
<i>Poa pratensis</i>	0.747	0.688
<i>Rumex crispus</i>	6.169	0.046
<i>Solanum carolinense</i>	1.842	0.398
<i>Solidago canadensis</i>	1.501	0.472
<i>Taraxacum officinale</i>	3.496	0.174
<i>Thlaspi arvense</i>	2.000	0.368

2003	$H_{3,3,3}$	P-value
<i>Ambrosia trifida</i>	1.199	0.549
<i>Aster ericoides</i>	1.156	0.561
<i>Bromus japonicus</i>	0.747	0.688
<i>Cirsium arvense</i>	0.157	0.925
<i>Dactylis glomerata</i>	0.622	0.733
<i>Festuca elatior</i>	3.467	0.177
<i>Galium asprellum</i>	0.157	0.925
<i>Geum canadense</i>	0.315	0.854
<i>Poa pratensis</i>	6.214	0.045
<i>Rumex crispus</i>	1.195	0.550
<i>Solanum carolinense</i>	1.114	0.573
<i>Solidago canadensis</i>	0.622	0.733
<i>Taraxacum officinale</i>	1.067	0.587
<i>Thlaspi arvense</i>	1.915	0.384

2004	$H_{3,3,3}$	P-value
<i>Ambrosia trifida</i>	1.167	0.558

<i>Aster ericoides</i>	2.575	0.276
<i>Bromus japonicus</i>	0.000	1.000
<i>Cirsium arvense</i>	4.392	0.111
<i>Dactylis glomerata</i>	2.575	0.276
<i>Festuca elatior</i>	1.689	0.430
<i>Galium asprellum</i>	0.125	0.939
<i>Geum canadense</i>	4.500	0.105
<i>Poa pratensis</i>	0.960	0.619
<i>Rumex crispus</i>	3.954	0.138
<i>Solanum carolinense</i>	2.715	0.257
<i>Solidago canadensis</i>	0.000	1.000
<i>Taraxacum officinale</i>	0.627	0.731
<i>Thlaspi arvense</i>	0.092	0.955

### 3. Late successional grassland

2002	$H_{3,3,3}$	P-value
<i>Barbarea vulgaris</i>	3.034	0.219
<i>Bromus inermis</i>	1.747	0.417
<i>Cirsium arvense</i>	0.089	0.957
<i>Festuca elatior</i>	6.489	0.039
<i>Pastinaca sativa</i>	0.356	0.837
<i>Poa pratensis</i>	1.681	0.432
<i>Solanum carolinense</i>	1.167	0.558
<i>Solidago canadensis</i>	3.289	0.193

2003	$H_{3,3,3}$	P-value
<i>Barbarea vulgaris</i>	1.167	0.558
<i>Bromus inermis</i>	0.356	0.837
<i>Cirsium arvense</i>	0.429	0.807
<i>Festuca elatior</i>	5.468	0.065
<i>Pastinaca sativa</i>	0.429	0.807
<i>Poa pratensis</i>	1.867	0.393
<i>Solanum carolinense</i>	2.000	0.368
<i>Solidago canadensis</i>	2.756	0.252

2004	$H_{3,3,3}$	P-value
<i>Barbarea vulgaris</i>	1.167	0.558
<i>Bromus inermis</i>	2.489	0.288
<i>Cirsium arvense</i>	0.560	0.756
<i>Festuca elatior</i>	5.600	0.061
<i>Pastinaca sativa</i>	2.489	0.288
<i>Poa pratensis</i>	3.200	0.202
<i>Solanum carolinense</i>	1.147	0.564
<i>Solidago canadensis</i>	3.289	0.193

## APPENDIX E.

Statistical tables for repeated measures ANOVA testing hypotheses regarding deer access (treatment) to plots in 1) early succession, 2) mid-succession, and 3) late succession.

### 1) Early succession

#### Forbs

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.118	1	0.118	2.356	0.200		
Error	0.200	4	0.050				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	1.380	6	0.230	10.283	0.000	0.004	0.000
period*TRMT\$	0.095	6	0.016	0.707	0.647	0.532	0.647
Error	0.537	24	0.022				

#### Graminoids

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.122	1	0.122	2.515	0.188		
Error	0.193	4	0.048				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	1.436	6	0.239	10.344	0.000	0.005	0.000
period*TRMT\$	0.095	6	0.016	0.681	0.667	0.542	0.665
Error	0.555	24	0.023				

### Woody seedlings (only 2004, 2005 data)

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.000	1	0.000	1.202	0.334		
Error	0.001	4	0.000				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.001	4	0.000	3.110	0.045	0.111	0.050
period*TRMT\$	0.000	4	0.000	1.520	0.244	0.279	0.247
Error	0.001	16	0.000				

#### Species richness

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	16.095	1	16.095	3.654	0.129		
Error	17.619	4	4.405				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	296.571	6	49.429	16.697	0.000	0.000	0.000
period*TRMT\$	7.238	6	1.206	0.408	0.867	0.718	0.867
Error	71.048	24	2.960				

#### Species evenness

Between Subjects						
Source	SS	df	MS	F	P	
TRMT\$	0.016	1	0.016	1.321	0.315	
Error	0.049	4	0.012			
Within Subjects						

Source	SS	df	MS	F	P	G-G	H-F
period	0.224	6	0.037	3.393	0.014	0.084	0.020
period*TRMT\$	0.019	6	0.003	0.286	0.938	0.763	0.922
Error	0.264	24	0.011				

### Gini diversity

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.003	1	0.003	0.193	0.683
Error	0.064	4	0.016		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
period	0.741	6	0.124	9.887	0.000	0.009	0.000
period*TRMT\$	0.051	6	0.008	0.678	0.669	0.523	0.618
Error	0.300	24	0.012				

## 2. Mid-succession

There were no woody seedlings.

### Forbs

#### Univariate and Multivariate Repeated Measures Analysis

##### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.525	1	0.525	8.007	0.047
Error	0.262	4	0.066		

##### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
period	0.547	7	0.078	21.947	0.000	0.000	0.000
period*TRMT\$	0.069	7	0.010	2.759	0.026	0.089	0.026
Error	0.100	28	0.004				

### Graminoids

#### Univariate and Multivariate Repeated Measures Analysis

##### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.538	1	0.538	8.106	0.047
Error	0.266	4	0.066		

##### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
period	0.535	7	0.076	21.214	0.000	0.000	0.000
period*TRMT\$	0.064	7	0.009	2.555	0.036	0.107	0.036
Error	0.101	28	0.004				

### Species richness

#### Between Subjects

Source	SS	df	MS	F	P
TRMT\$	0.750	1	0.750	0.172	0.699
Error	17.417	4	4.354		

#### Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
period	117.000	7	16.714	11.724	0.000	0.002	0.000
period*TRMT\$	13.583	7	1.940	1.361	0.260	0.306	0.260
Error	39.917	28	1.426				

### Species evenness

#### Between Subjects

Source	SS	df	MS	F	P
--------	----	----	----	---	---

TRMT\$	0.044	1	0.044	0.615	0.477		
Error	0.285	4	0.071				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.172	7	0.025	3.376	0.010	0.065	0.010
period*TRMT\$	0.050	7	0.007	0.982	0.464	0.428	0.464
Error	0.204	28	0.007				

### Gini diversity

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.129	1	0.129	1.275	0.322		
Error	0.405	4	0.101				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.338	7	0.048	5.991	0.000	0.022	0.001
period*TRMT\$	0.036	7	0.005	0.646	0.714	0.559	0.692
Error	0.225	28	0.008				

### 3. Late succession

#### Forbs

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.155	1	0.155	0.459	0.535		
Error	1.347	4	0.337				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.108	7	0.015	4.577	0.002	0.021	0.002
period*TRMT\$	0.035	7	0.005	1.489	0.212	0.265	0.212
Error	0.094	28	0.003				

#### Graminoids

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.172	1	0.172	0.502	0.518		
Error	1.369	4	0.342				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.106	7	0.015	4.035	0.004	0.031	0.004
period*TRMT\$	0.035	7	0.005	1.342	0.268	0.306	0.268
Error	0.105	28	0.004				

#### Woody seedlings (springs, summers only)

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.000	1	0.000	0.570	0.492		
Error	0.001	4	0.000				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
year	0.000	2	0.000	0.750	0.503	0.436	0.464
year*TRMT\$	0.000	2	0.000	0.895	0.446	0.398	0.419
Error	0.001	8	0.000				

#### Species richness

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	24.083	1	24.083	0.318	0.603		
Error	302.833	4	75.708				

Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	54.583	7	7.798	3.864	0.005	0.063	0.010
period*TRMT\$	11.917	7	1.702	0.844	0.561	0.469	0.543
Error	56.500	28	2.018				

### Species evenness

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.008	1	0.008	0.069		0.805	
Error	0.455	4	0.114				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.047	7	0.007	0.806	0.590	0.494	0.590
period*TRMT\$	0.081	7	0.012	1.398	0.245	0.298	0.245
Error	0.231	28	0.008				

### Gini diversity

Between Subjects							
Source	SS	df	MS	F	P		
TRMT\$	0.007	1	0.007	0.633		0.471	
Error	0.047	4	0.012				
Within Subjects							
Source	SS	df	MS	F	P	G-G	H-F
period	0.092	7	0.013	2.656	0.031	0.097	0.031
period*TRMT\$	0.036	7	0.005	1.036	0.429	0.411	0.429
Error	0.138	28	0.005				

## APPENDIX F.

Statistical values of Mann-Whitney analyses of individual plant species' response to deer access in 1) early succession, 2) mid-succession, and 3) late succession.

## 1. Early succession

2003	U <sub>3,3</sub>	P-value
<i>Conyza canadensis</i>	5.0	0.827
<i>Medicago sativa</i>	2.0	0.275
<i>Oxalis corniculata</i>	5.0	0.817
<i>Physalis subglabrata</i>	4.5	1.000
<i>Polygonum persicaria</i>	7.0	0.275
<i>Setaria italica</i>	4.0	0.827
<i>Sida spinosa</i>	4.5	1.000
<i>Solanum ptychanthum</i>	7.0	1.344

2004		
<i>Cirsium arvense</i>	2	0.268
<i>Conyza canadensis</i>	3	1
<i>Geum canadense</i>	4.5	1
<i>Medicago sativa</i>	1	0.127
<i>Oxalis corniculata</i>	4	0.827
<i>Physalis subglabrata</i>	2	0.246
<i>Polygonum persicaria</i>	6	0.513
<i>Setaria italica</i>	8	0.127
<i>Sida spinosa</i>	8	0.127

2005		
<i>Ambrosia trifida</i>	3.5	0.658
<i>Cirsium arvense</i>	4	0.827
<i>Conyza canadensis</i>	6	0.317
<i>Elymus canadensis</i>	3	0.487
<i>Geum canadense</i>	4.5	1
<i>Medicago sativa</i>	4	0.827
<i>Oxalis corniculata</i>	5	0.827
<i>Physalis subglabrata</i>	2.5	0.376
<i>Polygonum persicaria</i>	5	0.827
<i>Setaria italica</i>	8	0.127

## 2. Mid-succession

2003	U <sub>3,3</sub>	P-value
<i>Ambrosia trifida</i>	1.5	0.121
<i>Asclepias syriaca</i>	4.0	0.817
<i>Aster ericoides</i>	5.0	0.827
<i>Cirsium arvense</i>	4.5	1.000
<i>Dactylis glomerata</i>	7.0	0.275
<i>Festuca elatior</i>	3.0	0.513
<i>Galium asprellum</i>	6.0	0.513
<i>Geum canadense</i>	4.0	0.817

<i>Medicago sativa</i>	5.0	0.048
<i>Poa pratensis</i>	4.5	1.000
<i>Solidago canadensis</i>	2.0	0.275
<i>Taraxacum officinale</i>	1.0	0.127
<i>Thlaspi arvense</i>	4.5	1.000

## 2004

<i>Ambrosia trifida</i>	4.0	0.817
<i>Asclepias syriaca</i>	3.0	0.507
<i>Aster ericoides</i>	4.0	0.827
<i>Cirsium arvense</i>	4.5	1.000
<i>Dactylis glomerata</i>	7.0	0.268
<i>Festuca elatior</i>	8.0	0.127
<i>Galium asprellum</i>	7.5	0.121
<i>Geum canadense</i>	2.5	0.346
<i>Medicago sativa</i>	2.0	0.246
<i>Poa pratensis</i>	4.0	0.817
<i>Solidago canadensis</i>	2.0	0.275
<i>Taraxacum officinale</i>	7.0	0.275
<i>Thlaspi arvense</i>	2.0	0.268

## 2005

<i>Ambrosia trifida</i>	4.0	0.822
<i>Asclepias syriaca</i>	2.0	0.268
<i>Aster ericoides</i>	4.0	0.827
<i>Cirsium arvense</i>	2.5	0.376
<i>Dactylis glomerata</i>	6.0	0.487
<i>Festuca elatior</i>	9.0	0.050
<i>Galium asprellum</i>	7.5	0.121
<i>Geum canadense</i>	3.0	0.500
<i>Medicago sativa</i>	4.5	1.000
<i>Poa pratensis</i>	4.5	1.000
<i>Solidago canadensis</i>	3.0	0.513
<i>Taraxacum officinale</i>	8.5	0.068
<i>Thlaspi arvense</i>	3.0	0.507

## 3. Late succession

	$U_{3,3}$	P-value
2003		
<i>Barbarea vulgaris</i>	4.5	1.000
<i>Bromus inermis</i>	8.0	0.127
<i>Carex laevivaginata</i>	0.0	0.050
<i>Cirsium arvense</i>	4.0	0.827
<i>Festuca elatior</i>	4.0	0.048
<i>Lolium perenne</i>	4.0	0.817
<i>Pastinaca sativa</i>	3.0	0.513
<i>Poa pratensis</i>	5.0	0.827
<i>Solidago canadensis</i>	3.0	0.429

## 2004

<i>Barbarea vulgaris</i>	6.5	0.346
<i>Bromus inermis</i>	8.0	0.127



<i>Carex laevivaginata</i>	5.0	0.817
<i>Cirsium arvense</i>	1.0	0.127
<i>Festuca elatior</i>	6.0	0.513
<i>Pastinaca sativa</i>	3.0	0.513
<i>Poa pratensis</i>	6.5	0.369
<i>Solidago canadensis</i>	4.0	0.827

## 2005

<i>Barbarea vulgaris</i>	6.5	0.369
<i>Bromus inermis</i>	8.0	0.127
<i>Carex laevivaginata</i>	5.0	0.817
<i>Cirsium arvense</i>	2.0	0.268
<i>Festuca elatior</i>	2.0	0.275
<i>Pastinaca sativa</i>	5.0	0.827
<i>Poa pratensis</i>	8.0	0.127
<i>Solidago canadensis</i>	3.0	0.513

## APPENDIX G.

Means and standard errors for all plant species for fall seasons, 2001 through 2004 in the 1) early successional grassland, 2) mid-successional grassland, and 3) late successional grassland (no 2001 in early succession). Treatments are n (no deer access only), m (mouse and deer access), v (mouse, vole, and deer access), r (fenced control plots), f (unfenced control plots), d (no deer).

## 1. Early successional grassland

Year	2002									
Treatment	n		m		v		r		f	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Abutilon theophrasti</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.017	0.010	0.024	0.022
<i>Amaranthus retroflexus</i>	0.006	0.004	0.019	0.014	0.025	0.015	0.023	0.010	0.047	0.038
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Cirsium arvense</i>	0.022	0.022	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000
<i>Conyza canadensis</i>	0.117	0.041	0.305	0.134	0.220	0.110	0.363	0.168	0.208	0.085
<i>Digitaria sanguinalis</i>	0.412	0.082	0.357	0.181	0.365	0.158	0.440	0.167	0.399	0.170
<i>Echinochloa crus-galli</i>	0.002	0.002	0.013	0.013	0.007	0.007	0.015	0.009	0.003	0.002
<i>Elymus canadensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Chamaesyce maculata</i>	0.010	0.007	0.030	0.027	0.046	0.036	0.005	0.005	0.007	0.003
<i>Festuca elatior</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Geum canadense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.045	0.021	0.016	0.004	0.015	0.002	0.023	0.010	0.018	0.001
<i>Mollugo verticillata</i>	0.002	0.002	0.007	0.004	0.016	0.010	0.006	0.006	0.001	0.001
<i>Oxalis corniculata</i>	0.012	0.009	0.005	0.003	0.000	0.000	0.003	0.002	0.001	0.001
<i>Panicum capillare</i>	0.057	0.040	0.049	0.044	0.028	0.016	0.000	0.000	0.020	0.009
<i>Phleum pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Physalis subglabrata</i>	0.011	0.007	0.001	0.001	0.007	0.007	0.000	0.000	0.003	0.003
<i>Phytolacca americana</i>	0.000	0.000	0.003	0.003	0.003	0.003	0.003	0.002	0.007	0.007
<i>Toxicodendron rydbergii</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Polygonum persicaria</i>	0.107	0.096	0.113	0.060	0.140	0.081	0.030	0.012	0.182	0.104
<i>Portulaca oleracea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Setaria viridis</i>	0.186	0.055	0.048	0.023	0.039	0.017	0.055	0.016	0.051	0.020
<i>Sida spinosa</i>	0.045	0.034	0.005	0.005	0.018	0.006	0.014	0.008	0.020	0.004
<i>Solanum carolinense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solanum ptychanthum</i>	0.009	0.007	0.028	0.028	0.049	0.049	0.000	0.000	0.005	0.003
<i>Solidago canadensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Stellaria graminea</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2003											
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Abutilon theophrasti</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Amaranthus retroflexus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.006	0.006	0.012	0.003	0.003	0.003	0.007	0.007	0.000	0.000	0.000	0.000
<i>Cirsium arvense</i>	0.119	0.119	0.012	0.006	0.000	0.000	0.003	0.003	0.010	0.010	0.010	0.010
<i>Conyza canadensis</i>	0.554	0.152	0.708	0.054	0.570	0.156	0.610	0.060	0.774	0.036	0.740	0.070
<i>Digitaria sanguinalis</i>	0.006	0.006	0.001	0.001	0.052	0.052	0.000	0.000	0.000	0.000	0.000	0.000
<i>Echinochloa crus-galli</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Elymus canadensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002
<i>Chamaesyce maculata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.016	0.000	0.000	0.000	0.000
<i>Geum canadense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.000	0.000
<i>Medicago sativa</i>	0.019	0.008	0.031	0.017	0.004	0.004	0.001	0.001	0.004	0.003	0.037	0.033
<i>Mollugo verticillata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Oxalis corniculata</i>	0.009	0.007	0.014	0.005	0.006	0.001	0.006	0.002	0.000	0.000	0.003	0.002
<i>Panicum capillare</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Phleum pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Physalis subglabrata</i>	0.013	0.012	0.004	0.004	0.003	0.003	0.001	0.001	0.004	0.002	0.006	0.004
<i>Phytolacca americana</i>	0.000	0.000	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Toxicodendron rydbergii</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.008	0.008	0.000	0.000	0.000	0.000
<i>Polygonum persicaria</i>	0.009	0.007	0.003	0.003	0.001	0.001	0.003	0.003	0.019	0.006	0.002	0.002
<i>Portulaca oleracea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Setaria viridis</i>	0.249	0.113	0.196	0.059	0.343	0.096	0.324	0.081	0.171	0.026	0.163	0.061
<i>Sida spinosa</i>	0.008	0.006	0.001	0.001	0.007	0.002	0.001	0.001	0.006	0.004	0.005	0.002
<i>Solanum carolinense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solanum ptychanthum</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.007	0.007	0.000	0.000	0.009	0.009	0.009	0.007	0.000	0.000	0.008	0.008
<i>Stellaria graminea</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2004											
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Abutilon theophrasti</i>	0.000	0.000	0.000	0.000	0.003	0.002	0.010	0.004	0.021	0.001	0.004	0.001
<i>Amaranthus retroflexus</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.059
<i>Asclepias syriaca</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.020	0.017	0.009	0.004	0.003	0.003	0.004	0.002	0.006	0.006	0.018	0.018
<i>Cirsium arvense</i>	0.003	0.000	0.224	0.186	0.039	0.031	0.032	0.015	0.007	0.007	0.088	0.076
<i>Conyza canadensis</i>	0.000	0.000	0.022	0.022	0.002	0.001	0.002	0.001	0.006	0.004	0.002	0.001
<i>Digitaria sanguinalis</i>	0.097	0.050	0.144	0.055	0.150	0.049	0.084	0.030	0.149	0.065	0.066	0.062
<i>Echinochloa crus-galli</i>	0.000	0.000	0.004	0.004	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001
<i>Elymus canadensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.029	0.029
<i>Chamaesyce maculata</i>	0.000	0.000	0.000	0.000	0.012	0.004	0.000	0.000	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.017	0.026	0.013	0.000	0.000
<i>Geum canadense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.006	0.003
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000
<i>Medicago sativa</i>	0.082	0.038	0.082	0.016	0.049	0.021	0.078	0.011	0.064	0.018	0.130	0.062
<i>Mollugo verticillata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Oxalis corniculata</i>	0.002	0.002	0.000	0.000	0.000	0.000	0.002	0.001	0.002	0.001	0.001	0.001
<i>Panicum capillare</i>	0.003	0.003	0.024	0.004	0.032	0.031	0.000	0.000	0.026	0.013	0.017	0.011
<i>Phleum pratense</i>	0.000	0.000	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000	0.000	0.000
<i>Physalis subglabrata</i>	0.002	0.002	0.003	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.009	0.006
<i>Phytolacca americana</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Toxicodendron rydbergii</i>	0.007	0.007	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Polygonum persicaria</i>	0.018	0.018	0.020	0.014	0.036	0.019	0.017	0.004	0.040	0.026	0.080	0.045
<i>Portulaca oleracea</i>	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Setaria viridis</i>	0.747	0.093	0.405	0.099	0.548	0.072	0.673	0.037	0.588	0.101	0.413	0.085
<i>Sida spinosa</i>	0.013	0.013	0.003	0.002	0.014	0.003	0.006	0.004	0.021	0.009	0.011	0.008
<i>Solanum carolinense</i>	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solanum ptychanthum</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.005	0.002	0.048	0.031	0.101	0.036	0.069	0.025	0.021	0.004	0.052	0.028
<i>Stellaria graminea</i>	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.007	0.007
<i>Verbena urticifolia</i>	0.000	0.000	0.002	0.002	0.001	0.001	0.001	0.001	0.010	0.010	0.006	0.003

## 2. Mid-successional grassland

Year	2001									
Treatment	n		m		v		r		f	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.008	0.008	0.001	0.001	0.006	0.003	0.001	0.001	0.000	0.000
<i>Asclepias syriaca</i>	0.007	0.007	0.006	0.006	0.000	0.000	0.000	0.000	0.006	0.006
<i>Aster ericoides</i>	0.034	0.015	0.022	0.017	0.038	0.024	0.068	0.040	0.024	0.015
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus japonicus</i>	0.076	0.021	0.088	0.017	0.038	0.023	0.038	0.020	0.042	0.037
<i>Cirsium arvense</i>	0.008	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002
<i>Dactylis glomerata</i>	0.068	0.021	0.006	0.006	0.091	0.091	0.082	0.074	0.077	0.070
<i>Elymus canadensis</i>	0.000	0.000	0.000	0.000	0.014	0.014	0.036	0.036	0.000	0.000
<i>Festuca elatior</i>	0.164	0.036	0.249	0.046	0.198	0.076	0.143	0.035	0.261	0.026
<i>Geum canadense</i>	0.004	0.004	0.002	0.001	0.006	0.001	0.010	0.003	0.023	0.013
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000
<i>Medicago sativa</i>	0.232	0.024	0.208	0.048	0.253	0.056	0.259	0.076	0.290	0.024
<i>Morus alba</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Phleum pratense</i>	0.017	0.017	0.032	0.032	0.000	0.000	0.010	0.006	0.000	0.000
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Plantago major</i>	0.002	0.002	0.003	0.000	0.001	0.001	0.003	0.003	0.001	0.001
<i>Poa pratensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.000	0.000
<i>Polygonum persicaria</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rumex crispus</i>	0.003	0.003	0.006	0.001	0.002	0.002	0.003	0.000	0.000	0.000
<i>Setaria italica</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.003	0.000	0.000
<i>Solidago canadensis</i>	0.339	0.009	0.341	0.068	0.307	0.078	0.289	0.093	0.237	0.035
<i>Taraxacum officinale</i>	0.008	0.003	0.004	0.003	0.014	0.013	0.018	0.006	0.013	0.009
<i>Thlaspi arvense</i>	0.000	0.000	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.001	0.001	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2002									
Treatment	n		m		v		r		f	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.001	0.001	0.002	0.002	0.006	0.004	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.010	0.010	0.008	0.008	0.000	0.000	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.032	0.017	0.043	0.024	0.026	0.014	0.150	0.076	0.040	0.012
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.003	0.003	0.001	0.001	0.000	0.000
<i>Bromus inermis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus japonicus</i>	0.000	0.000	0.007	0.005	0.018	0.013	0.014	0.014	0.000	0.000
<i>Cirsium arvense</i>	0.006	0.006	0.002	0.001	0.008	0.008	0.003	0.003	0.005	0.002
<i>Dactylis glomerata</i>	0.107	0.046	0.019	0.012	0.142	0.120	0.112	0.083	0.138	0.138
<i>Elymus canadensis</i>	0.020	0.020	0.006	0.006	0.000	0.000	0.110	0.110	0.000	0.000
<i>Festuca elatior</i>	0.186	0.078	0.259	0.017	0.174	0.050	0.069	0.024	0.250	0.126
<i>Geum canadense</i>	0.000	0.000	0.006	0.003	0.006	0.001	0.013	0.011	0.001	0.001
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.274	0.025	0.168	0.094	0.126	0.026	0.134	0.055	0.300	0.022
<i>Morus alba</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Phleum pratense</i>	0.042	0.042	0.029	0.021	0.000	0.000	0.003	0.003	0.000	0.000
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Plantago major</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.011	0.011	0.000	0.000	0.000	0.000	0.001	0.001	0.004	0.004
<i>Polygonum persicaria</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rumex crispus</i>	0.000	0.000	0.008	0.007	0.001	0.001	0.001	0.001	0.001	0.001
<i>Setaria italica</i>	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.283	0.032	0.399	0.121	0.469	0.093	0.380	0.085	0.250	0.049
<i>Taraxacum officinale</i>	0.018	0.002	0.006	0.003	0.006	0.003	0.009	0.006	0.009	0.003
<i>Thlaspi arvense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2003											
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.004	0.004	0.006	0.003	0.009	0.004	0.000	0.000	0.000	0.000	0.006	0.006
<i>Asclepias syriaca</i>	0.001	0.001	0.006	0.006	0.001	0.001	0.006	0.006	0.020	0.020	0.009	0.007
<i>Aster ericoides</i>	0.031	0.016	0.023	0.012	0.060	0.030	0.232	0.117	0.077	0.028	0.091	0.066
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.008	0.008	0.002	0.002	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.062	0.041	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002
<i>Bromus japonicus</i>	0.000	0.000	0.007	0.007	0.002	0.002	0.000	0.000	0.000	0.000	0.002	0.002
<i>Cirsium arvense</i>	0.014	0.009	0.021	0.016	0.006	0.006	0.018	0.016	0.002	0.002	0.013	0.007
<i>Dactylis glomerata</i>	0.097	0.015	0.004	0.002	0.040	0.032	0.040	0.011	0.131	0.118	0.000	0.000
<i>Elymus canadensis</i>	0.014	0.014	0.000	0.000	0.007	0.007	0.054	0.048	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.291	0.045	0.251	0.104	0.172	0.021	0.109	0.025	0.341	0.113	0.242	0.050
<i>Geum canadense</i>	0.001	0.001	0.006	0.006	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.133	0.017	0.022	0.021	0.015	0.006	0.028	0.007	0.051	0.011	0.062	0.042
<i>Morus alba</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Phleum pratense</i>	0.011	0.011	0.003	0.003	0.000	0.000	0.002	0.002	0.000	0.000	0.007	0.007
<i>Physalis subglabrata</i>	0.000	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.002	0.002	0.000	0.000
<i>Plantago major</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.008	0.008	0.000	0.000	0.009	0.009	0.007	0.007	0.006	0.006	0.000	0.000
<i>Polygonum persicaria</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rumex crispus</i>	0.003	0.003	0.011	0.006	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Setaria italica</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.311	0.030	0.603	0.099	0.646	0.040	0.496	0.119	0.348	0.057	0.563	0.146
<i>Taraxacum officinale</i>	0.011	0.001	0.018	0.006	0.006	0.002	0.004	0.001	0.004	0.003	0.002	0.002
<i>Thlaspi arvense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.017	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2004											
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.006	0.006	0.000	0.000	0.012	0.012	0.000	0.000	0.002	0.002	0.002	0.001
<i>Asclepias syriaca</i>	0.000	0.000	0.010	0.010	0.006	0.006	0.010	0.010	0.016	0.016	0.003	0.003
<i>Aster ericoides</i>	0.068	0.043	0.003	0.003	0.064	0.029	0.200	0.101	0.093	0.027	0.185	0.122
<i>Barbarea vulgaris</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.052	0.052	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus japonicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Cirsium arvense</i>	0.003	0.003	0.022	0.016	0.040	0.025	0.030	0.023	0.030	0.027	0.020	0.010
<i>Dactylis glomerata</i>	0.057	0.018	0.012	0.008	0.027	0.023	0.047	0.044	0.080	0.080	0.002	0.002
<i>Elymus canadensis</i>	0.016	0.016	0.000	0.000	0.000	0.000	0.008	0.008	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.389	0.024	0.071	0.039	0.048	0.014	0.072	0.043	0.302	0.089	0.144	0.034
<i>Geum canadense</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.073	0.019	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Morus alba</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.004	0.001	0.001
<i>Phleum pratense</i>	0.011	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Physalis subglabrata</i>	0.000	0.000	0.001	0.001	0.001	0.001	0.000	0.000	0.001	0.001	0.000	0.000
<i>Plantago major</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.002	0.002	0.022	0.022	0.007	0.004
<i>Polygonum persicaria</i>	0.000	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rumex crispus</i>	0.001	0.001	0.007	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Setaria italica</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.299	0.074	0.834	0.045	0.792	0.041	0.631	0.182	0.450	0.057	0.635	0.144
<i>Taraxacum officinale</i>	0.007	0.007	0.006	0.003	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Thlaspi arvense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Verbena urticifolia</i>	0.000	0.000	0.012	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000



## 3. Late successional grassland

Year	2001									
Treatment	n		m		v		r		f	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.007	0.007	0.000	0.000	0.017	0.015	0.004	0.003	0.003	0.003
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.001	0.001	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus japonicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Calystegia sepium</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Cirsium arvense</i>	0.016	0.014	0.010	0.007	0.017	0.012	0.016	0.005	0.021	0.009
<i>Elaeagnus angustifolia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.661	0.019	0.568	0.058	0.544	0.084	0.712	0.066	0.606	0.130
<i>Geum canadense</i>	0.000	0.000	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001
<i>Lolium perenne</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.000	0.000	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000
<i>Morus alba</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.026	0.012	0.050	0.038	0.066	0.028	0.042	0.005	0.092	0.039
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.062	0.008	0.061	0.024	0.096	0.068	0.083	0.053	0.039	0.008
<i>Prunus serotina</i>	0.001	0.001	0.001	0.001	0.002	0.002	0.000	0.000	0.000	0.000
<i>Rosa multiflora</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rubus occidentalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.008	0.001	0.001
<i>Solanum carolinense</i>	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.203	0.020	0.276	0.032	0.216	0.051	0.113	0.026	0.200	0.077
<i>Taraxacum officinale</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.001	0.001
<i>Trifolium pratense</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.001	0.001
<i>Vernonia gigantea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Viola affinis</i>	0.000	0.000	0.000	0.000	0.016	0.016	0.001	0.001	0.004	0.004
<i>Vitis palmata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000

Year	2002									
Treatment	n		m		v		r		f	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.000	0.000	0.005	0.003	0.000	0.000	0.001	0.001	0.000	0.000
<i>Aster ericoides</i>	0.002	0.002	0.000	0.000	0.001	0.001	0.003	0.003	0.000	0.000
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.090	0.034	0.040	0.040	0.235	0.087	0.262	0.127	0.275	0.098
<i>Bromus japonicus</i>	0.000	0.000	0.013	0.013	0.000	0.000	0.000	0.000	0.000	0.000
<i>Calystegia sepium</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007	0.000	0.000
<i>Cirsium arvense</i>	0.030	0.025	0.032	0.019	0.018	0.011	0.014	0.003	0.028	0.016
<i>Elaeagnus angustifolia</i>	0.000	0.000	0.000	0.000	0.009	0.009	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.526	0.028	0.359	0.030	0.241	0.014	0.408	0.075	0.329	0.085
<i>Geum canadense</i>	0.000	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Lolium perenne</i>	0.001	0.001	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Morus alba</i>	0.000	0.000	0.008	0.008	0.002	0.002	0.002	0.002	0.006	0.003
<i>Pastinaca sativa</i>	0.024	0.012	0.039	0.019	0.077	0.040	0.033	0.014	0.049	0.024
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.019	0.019	0.048	0.048	0.106	0.030	0.061	0.020	0.033	0.030
<i>Prunus serotina</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rosa multiflora</i>	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rubus occidentalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.015	0.000	0.000
<i>Solanum carolinense</i>	0.000	0.000	0.000	0.000	0.002	0.001	0.002	0.001	0.000	0.000
<i>Solidago canadensis</i>	0.300	0.068	0.433	0.083	0.288	0.027	0.192	0.043	0.278	0.092
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.015	0.015	0.000	0.000	0.000	0.000	0.000	0.000
<i>Viola affinis</i>	0.000	0.000	0.000	0.000	0.021	0.021	0.000	0.000	0.000	0.000
<i>Vitis palmata</i>	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Year	2003											
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Asclepias syriaca</i>	0.000	0.000	0.006	0.004	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.028	0.028
<i>Barbarea vulgaris</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.132	0.017	0.110	0.091	0.175	0.078	0.195	0.097	0.194	0.099	0.077	0.072
<i>Bromus japonicus</i>	0.000	0.000	0.004	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Calystegia sepium</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.000	0.000	0.001	0.001
<i>Cirsium arvense</i>	0.027	0.023	0.023	0.010	0.020	0.017	0.011	0.004	0.012	0.005	0.024	0.010
<i>Elaeagnus angustifolia</i>	0.000	0.000	0.000	0.000	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.608	0.018	0.461	0.042	0.345	0.131	0.575	0.120	0.469	0.035	0.463	0.029
<i>Geum canadense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Lolium perenne</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Morus alba</i>	0.000	0.000	0.010	0.010	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.021	0.007	0.028	0.019	0.046	0.020	0.023	0.006	0.059	0.004	0.130	0.062
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Poa pratensis</i>	0.020	0.017	0.046	0.038	0.122	0.036	0.128	0.059	0.040	0.020	0.023	0.013
<i>Prunus serotina</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000
<i>Rosa multiflora</i>	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Rubus occidentalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.013	0.000	0.000	0.000	0.000
<i>Solanum carolinense</i>	0.000	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.172	0.050	0.310	0.061	0.283	0.059	0.050	0.021	0.220	0.131	0.250	0.027
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Viola affinis</i>	0.000	0.000	0.000	0.000	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vitis palmata</i>	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.001	0.001

Year	2004		SE									
Treatment	n		m		v		r		f		d	
Species	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
<i>Ambrosia trifida</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Asclepias syriaca</i>	0.000	0.000	0.004	0.002	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Aster ericoides</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.027	0.025
<i>Barbarea vulgaris</i>	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Bromus inermis</i>	0.130	0.013	0.089	0.058	0.191	0.088	0.114	0.068	0.113	0.057	0.031	0.028
<i>Bromus japonicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Calystegia sepium</i>	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000	0.000	0.000	0.002	0.002
<i>Cirsium arvense</i>	0.009	0.006	0.021	0.013	0.026	0.021	0.018	0.013	0.003	0.002	0.028	0.018
<i>Elaeagnus angustifolia</i>	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Festuca elatior</i>	0.660	0.009	0.293	0.125	0.220	0.081	0.591	0.055	0.617	0.087	0.530	0.032
<i>Geum canadense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gleditsia triacanthos</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Lolium perenne</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Medicago sativa</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Morus alba</i>	0.000	0.000	0.007	0.005	0.004	0.004	0.001	0.001	0.000	0.000	0.000	0.000
<i>Pastinaca sativa</i>	0.010	0.005	0.013	0.005	0.032	0.017	0.016	0.003	0.040	0.007	0.070	0.039
<i>Physalis subglabrata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.004
<i>Poa pratensis</i>	0.003	0.003	0.023	0.020	0.094	0.019	0.164	0.066	0.024	0.013	0.027	0.014
<i>Prunus serotina</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rosa multiflora</i>	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001
<i>Rubus occidentalis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.023	0.000	0.000	0.000	0.000
<i>Solanum carolinense</i>	0.001	0.001	0.004	0.003	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000
<i>Solidago canadensis</i>	0.176	0.011	0.540	0.185	0.428	0.154	0.072	0.022	0.201	0.134	0.273	0.032
<i>Taraxacum officinale</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Trifolium pratense</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vernonia gigantea</i>	0.000	0.000	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Viola affinis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Vitis palmata</i>	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.007	0.007

## CURRICULUM VITAE

**Carrie E. DeJaco**

### EDUCATION

- Ph. D. Candidate, (expect to defend Spring, 2006), University of Illinois at Urbana-Champaign, Program of Ecology and Evolutionary Biology. Advisor: Dr. George O. Batzli
- M.S. in Biology, 2000, University of Louisville, Department of Biology. Advisor: Dr. R. Jan Stevenson
- B.A. in Biology with Spanish minor, 1996, University of Louisville

### TEACHING

#### University of Illinois (2000-2005)

##### Awards and Recognition

- Incomplete List of Teachers Ranked Excellent, 2001-2005
- John G. & Evelyn Hartman Heiligenstein Outstanding Teaching Assistant Award, 2004

##### Teaching Assistant (10 semesters)

- led discussion sections to explore and clarify concepts from lecture
  - Introductory Biology
  - Genetics, Evolution, and Biodiversity
  - Ecology and Organismic Biology
  - Organismal and Evolutionary Biology, "Merit" section
- led experiments and activities in lab and field to complement lecture material
  - Introduction to Plants
  - Genetics, Evolution, and Biodiversity
  - Ecology and Organismic Biology
  - Ecology

##### Other

- organized graduate discussion seminar, Topics in Ecology and Evolution: Herbivory across the Animal Kingdom
- supervised and mentored 15 undergraduate field research assistants

#### University of Louisville (1997-2000)

##### Teaching Assistant (9 semesters)

- introduced and led experiments and activities in lab and field
  - Introduction to Biology
  - Introduction to Plants- assisted with design of labs for this new course
  - Introduction to Ecology- designed new lab activities for this course

### RESEARCH

#### Grants and Awards

##### University of Illinois

- 2005 Francis M. and Harlie M. Clark Research Support Grant, \$1100.
- Summer Research Award, \$500.

- Conference Travel Grant, \$200
- Conference Travel Grant, Graduate College, \$150
- Travel Grant, \$250.
- 2003 American Society of Mammalogists, \$1500.
- Summer Research Award, \$1000.
- 2002 American Society of Mammalogists, \$1000.
- University of Louisville**
- 2000 Graduate School Travel Grant, \$100.
- 1999 Department of Biology Research Grant, \$1000.
- Graduate School Travel Grant, \$100.
- 1996 Stuart E. Neff Award, University of Louisville.

### **Scholarships**

#### **University of Louisville**

- 1995, 1996 Commonwealth Scholarship

### **Experience**

#### **University of Illinois (2001-2005)**

- Ph. D. research
  - used experimental exclosures to test effects of removal mammalian herbivores on the vegetation and community development in old-fields of central Illinois
  - used feeding trials to determine food preferences of small herbivores
  - used greenhouse experiments to study seed dispersal of rabbits (via their scat)
- Research Assistant for long-term experiment to test effects of habitat fragmentation on local populations of prairie voles

#### **University of Louisville (1995-1999)**

- M.S. research: analyzed algal communities in tropical rain forest of Puerto Rico
- Research Assistantships
  - assisted in major study of streams in Kentucky and Indiana (water quality, periphyton, and macroinvertebrates)
  - enumerated and identified soft and diatomaceous algae collected nationwide
  - assisted with assessment of algal productivity in salt marshes of North Carolina
  - assisted in experiments with caddisfly larvae in artificial streams in Michigan
  - assisted in experiments to biologically reduce nitrate output of landfills
- Field Course: rain forest, coastal forest, and montane cloud forest of Costa Rica

### **Presentations and Abstracts**

- DeJaco, C. E. and G. O. Batzli. 2005. The influence of endozoochory by rabbits on early successional grasslands. Ecological Society of America, Montreal, QC, Canada.
- DeJaco, C. E. and G. O. Batzli. 2005. The influence of endozoochory by rabbits on early

- successional grasslands. American Society of Mammalogists, Springfield, MO.
- DeJaco, C. E. 2004. How do small mammals influence changes in plant communities? Illinois Biological Society, University of Illinois.
- DeJaco, C. E. and G. O. Batzli. 2003. Influence of small mammals on old field succession to grassland. American Society of Mammalogists, Lubbock, TX.
- DeJaco, C. E. and G. O. Batzli. 2003. Influence of small mammals on old field succession to grassland. Environmental Horizons, University of Illinois.
- DeJaco, C. E. and R. J. Stevenson. 2000. Analysis of algal communities throughout a tropical watershed. North American Benthological Society, Keystone, CO.
- DeJaco, C. E. and R. J. Stevenson. 1999. Characterization of algal communities throughout a watershed in the Caribbean National Forest, Puerto Rico. North American Diatom Symposium, Pingree Park, CO.

### **Theses and Manuscripts**

- DeJaco, C. E. and G. O. Batzli. In prep. Combined effects of herbivory and granivory by rodents in old-field grasslands. (for submission to the Journal of Mammalogy)
- DeJaco, C. E. and G. O. Batzli. In prep. Do rabbits affect succession of old-field grasslands? (for submission to the Journal of Mammalogy)
- DeJaco, C. E. and R. J. Stevenson. In prep. Diversity of algal communities throughout a tropical watershed in Puerto Rico. (for submission to the Journal of Phycology)
- DeJaco, C. E.. 2000. Characterization and analysis of algal communities throughout a watershed in Puerto Rico, Master's thesis, University of Louisville.

### **SERVICE**

#### **University of Illinois**

Graduate Students in Ecology and Evolution

2003-2004 President

2000-2002 Treasurer

Graduate Students' Symposium

2005 Student judge of poster presentations

2002-2003 Chair of the Planning Committee

2000-2006 Member of the Planning Committee

Department of Animal Biology

2003-2005 Student representative on the Graduate Program Committee

School of Integrative Biology

2003-2005 Panelist for Orientation of new Teaching Assistants

#### **University of Louisville**

Biology Graduate Students' Association

1999-2000 Member of the Benefits Committee

1998-1999 Vice-president/Treasurer

Department of Biology

1999-2000 Student representative on the Instructional Program Committee

1998-1999 Student representative on the Faculty Search Committee